DOCTORAL THESIS

Social resilience and stress reactivity in chacma baboons

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Award date:
2020

Awarding institution:
University of Roehampton

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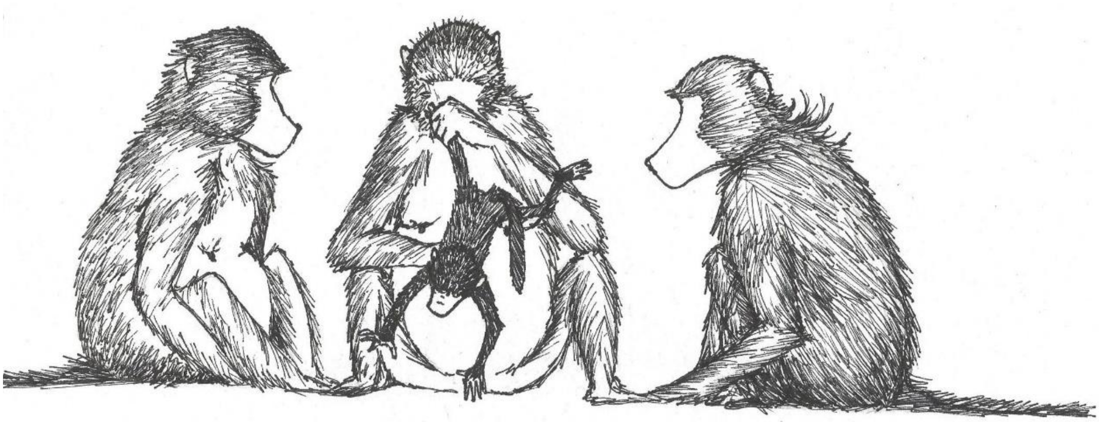

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by

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A thesis submitted in partial fulfilment of the requirements for the degree of PhD

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2019

Abstract

Resilience describes an individual’s ability to “rebound” after experiencing adversity and can be studied using the ‘three-hit concept’, where genetic factors (hit-1) interact with the early-life environment (hit-2), with the resulting phenotype’s resilience depending on later-in-life environment (hit-3). I investigated resilience and stress reactivity in a group of wild chacma baboons in South Africa, by exploring the different steps involved in the process of resilience: (i) describing physiological stress response measures and their link to life-history stage, climate, and predation; (ii) investigating coping behaviours and sociability and their link to physiological stress response measures; and (iii) developing non-invasive measures of resilience (based on the difference between individuals’ observed and predicted coat condition given their stress reactivity) and exploring links between resilience and coping behaviours and sociability.

Mean faecal glucocorticoid metabolite (fGCM) levels differed between life-history stages, and females, but not males, showed increased fGCM levels in response to predation. Furthermore, baboons of both sexes used displacement behaviours as coping behaviour in response to adversity, and rates of giving grooming in males, and rates of being aggressive in females, were linked to physiological stress response measures in the longer term. Females appeared to benefit from having strong social bonds as these were linked to lower mean fGCM levels, reflecting social buffering, while social integration was linked to lower stress reactivity in both sexes. Finally, resilience differed with life-history stages in females, but not males, and was linked to reproductive success in females. In both sexes, resilience might be behaviourally mediated, as high rates of displacement behaviours were associated with higher resilience, and in females, social integration was also linked to higher resilience. This study contributes conceptually and methodologically by developing non-invasive measures of resilience, thus enabling further investigation of resilience in the context of inter-individual differences in fitness in wild animals.

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ACTH	Adrenocorticotropic hormone
CI	(95%-) Confidence interval
CRH	Corticotropin-releasing hormone
CSI	Composite Sociality Index (dyadic)
DRS	Demonstrated reactive scope
DRS_{CV}	Coefficient of variation of the demonstrated reactive scope
EIA	Enzyme immunoassay
fGCM	Faecal glucocorticoid metabolite
GC	Glucocorticoid
HPA-axis	Hypothalamic-pituitary-adrenal axis
IQR	Inter-quartile range
IRT	Infrared thermography
LM	General linear model
LMM	General linear mixed model
R_{change}	Resilience based on the change in coat condition given an individual's DRS_{CV}
R_{coat}	Resilience based on the average coat condition given an individual's DRS_{CV}
R_{temp}	Resilience based on delta coat temperature given an individual's DRS_{CV}
uGCM	Urinary glucocorticoid metabolite

Acknowledgements

This thesis would not exist without the help and support of many people.

First and foremost, I would like to express my gratitude to my supervisors, Prof Ann MacLarnon and Prof Stuart Semple, for their guidance and support throughout this project. They have immensely helped with project design, supported me during data collection and laboratory analyses, and advised me on data analysis and interpretation, as well as gave me valued feedback during the writing of the actual thesis. I have learned immensely from our discussions of theoretical and practical issues and you have shaped my scientific thinking more than I would have expected. Thank you very much!

I would also like to thank Prof Russell Hill for allowing me to collect data on the baboons at the Primate and Predator Project study site in South Africa when I was in desperate need of a new field site. While fieldwork was a difficult time, it was all made easier by knowing that so many people had my back, both in the field and at home. I would especially like to thank the management team of Lajuma research station, Bibi and Jabu Linden and Kyle Stuart, for all your practical and emotional support, your wisdom, and your friendship. I would also like to thank the managers of the Primate and Predator Project, Leah, Andy, and Phil, for the successful collaboration and companionship. I am very grateful to the local staff as well, especially Hilda and Ticha and all those who had to schlepp around heavy gas bottles for me – you are what keeps this field site running! Furthermore, thank you to Stefanie and André Ganswindt from the University of Pretoria for your practical support and advice.

I am grateful to have met some great people during my time at Lajuma, and I would like to thank the other PhD students and field assistants for the comradery in the

field (with special thanks to Sandi and Alice for your friendship). Most of all though, I am forever grateful to my amazing field assistant Allison Stitt – thank you so much for all your hard work and practical help, your never-ending support, the commiserating and celebrating, the days in the rain and in the heat, for all your input and, most importantly, for your friendship. I know it wasn't easy, so thank you for sticking with me. This thesis would not exist without you!

I would also like to express my gratitude to Balbir Singh Josen for all the training, help, and patience in the hormone laboratory; without you the hormone analysis would not have been possible. I am also grateful to Mary Mackenzie for the practical help in preparing for field work and throughout my time at Roehampton, as well as the remaining technical staff who were always very kind to me. I also thank the members of the Centre for Research in Evolutionary, Social, and Interdisciplinary Anthropology, for instructive seminars, for creating an enjoyable environment in which to conduct research, and for all the interesting discussions in King's Head.

A big thanks to my PhD colleagues and friends from the University of Roehampton. A special thanks to Paddy, Aleks, Phil, Dami, Eva, Mel, Simona, Tessa, Nakul, Christle and Nacho, as well as Marie-Claire, Natalia, Christina, and Simone for making me feel at home in London and teaching me the value of perseverance. Also thank you to the girls and guys from the psychology office, who welcomed me into their midst when there was no room anywhere else. Thanks to Piotr, for the comradery, help, and good discussions we had over the years!

While conducting a PhD can be an isolating experience, my friends from home were never more than a phone call away. Thank you, Kathie, for your friendship and your visit in South Africa which was a silver lining during a difficult time. And I am

immensely grateful to Nicole, for checking in on me when needed, for proofreading and giving feedback, for interesting monkey discussions, and for generally being an amazing friend.

And finally, a massive thank you to my family. Mama, Papa, Anna: vielen Dank für all eure Unterstützung, sei sie praktisch, finanziell oder emotional, fürs Beherbergen und Versorgen, für eure Geduld und euer Verständnis. Ohne euch wäre nichts hiervon möglich gewesen!

Funding

This research was supported by a Vice-Chancellor’s Scholarship. Additional funds for field research were provided by the German Primatological Society (Gesellschaft für Primatologie e.V.) via the Christian-Vogel-Fond für Freilandforschung. I am very grateful for the support.

1. General introduction

In the early 20th century, Eugène N. Marais observed that „the life of the baboon is in fact one continual nightmare of anxiety“ (Marais, 1975). This was based on his observations of the high occurrence of leopard attacks on the baboons in the Waterberg mountains in South Africa. Just as he described in baboons, all primate species experience severe stressors over their lifetime as well as the everyday social and environmental challenges that are connected to mediating one’s environment and surviving and reproducing while competing for resources. While all extant species developed their current state under natural selection, individuals even of the same population may differ significantly in their ability to cope with these challenges (Romero and Wingfield, 2015). Based on this variation, the concepts of ‘resilience’ and ‘vulnerability’ have been developed (Rutter, 1987), with individuals that are better able to cope with adversity being termed more resilient. While resilience represents one cornerstone of psychiatric thinking regarding differential responses to trauma in humans (Karatsoreos and McEwen, 2011), the concept of resilience as a process has not been well-defined or comprehensively studied in wild animals. Therefore, this thesis aims at defining and describing resilience in wild chacma baboons, an ideal study species in the context of stress and anxiety as Marais described.

The study will follow a three-part approach, with each of the three results chapters representing one step in the process of resilience. After describing important concepts around stress and resilience in this introductory chapter and giving an overview of general methodology in chapter 2, in chapter 3 I investigate physiological stress response measures, i.e. mean physiological stress response levels and stress reactivity, and how they link to demography, climate, and predation. In Chapter 4 I then examine coping behaviours as the behavioural responses to adversity that might help individuals cope with challenges, as well as social buffering as a longer-term mechanism for mitigating individuals' physiological stress response levels. In Chapter 5 I explore the concept of resilience in wild animals, develop new measures of resilience reflecting the 'success' of coping with everyday stressors, and link these to demographic, reproductive, behavioural, and social characteristics. These three steps in the process of resilience will also be reflected in the introduction, where I will first present the concepts linked to stress and stress reactivity, then describe the concept of coping and social buffering, and finally outline the concept of resilience and its applicability in studies of wild animals. While this general introduction will focus on the conceptual background, further details on previous empirical research regarding specific areas will be given in the respective chapters. Finally, in the general discussion chapter, I describe emerging questions which link the findings of the different chapters and their relevance.

1.1 Stress and stress reactivity

1.1.1 The physiology of the general stress response

Hormonal systems present integral mechanisms which effect the adjustment of behaviour, physiology, and morphological phenotypes to a changing environment (Nelson, 2005). Glucocorticoid (GC) hormones, for example, namely cortisol or corticosterone, are a very important part of vertebrates' hormone systems related to the maintenance of energy balance in organisms and thus a key element of organismal responses to predictable and unpredictable circumstances (Sapolsky et al., 2000). Circulating hormone levels or the magnitude of hormonal responses can vary significantly between and within individuals, and this can reflect differential fitness.

There are also other additional levels of phenotypic variation in hormonal systems that might have fitness implications, such as the distribution and abundance of hormone receptors, and the plasticity of hormonal responses (Hau et al., 2016). However, as the latter two are difficult to investigate in intact animals, I will focus here solely on circulating hormone levels.

Physiologically, the stress response is an evolutionarily conserved pathway that all vertebrates have in common. Besides the very rapid reaction of the so-called *fight-or-flight response* which is mediated mainly by epinephrine (adrenaline), the *general adaptation syndrome* or *stress response* leads within minutes to profound physiological and behavioural changes (Nelson, 2005). The main (and here simplified) pathway of the stress response is the Hypothalamic-Pituitary-Adrenal (HPA) axis, that leads to the synthesis of GCs from cholesterol (Nelson, 2005). GCs are mainly produced in the adrenal cortices, but can also be excreted from other tissues like the brain, lymph nodes, intestines, skin, and maybe even the heart, where local concentrations might vary from circulating hormone levels (Taves et al., 2011; Rensel and Schlinger, 2016). External and internal stimuli are integrated in the brain and lead to the secretion of neuropeptides, such as corticotropin releasing hormone (CRH) from the hypothalamus, within a few seconds (Hau et al., 2016). CRH, and possibly other mediators such as vasopressin, oxytocin, arginine, and mesotocin, in turn stimulate the secretion of adrenocorticotropic hormone (ACTH) from the pituitary gland (Wingfield and Romero, 2001). It takes about 15 seconds until the release of ACTH (Nelson, 2005), which then acts on enzymes in adrenocortical cells and leads within a few minutes to the synthesis and secretion of GCs (Hau et al., 2016). A schematic depiction of the HPA-axis and the phenotypic actions of GCs (from Hau et al., 2016) is shown in Figure 1.1.

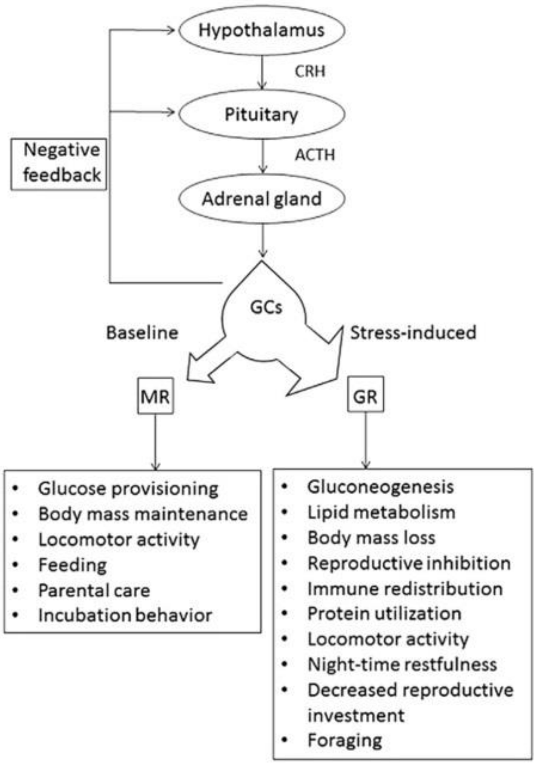


Figure 1.1 Schematic depiction of the Hypothalamic-Pituitary-Adrenal (HPA) axis, with activation leading to glucocorticoid (GC) production which results in several possible phenotypic actions. CRH: corticotropin-releasing hormone; ACTH: adrenocorticotropic hormone; MR: mineralocorticoid receptor; GR: glucocorticoid receptor. Negative feedback might occur at several stages of the HPA-axis.

Reprinted from Advances in the Study of Behavior, vol. 48, Hau, M., Casagrande, S., Ouyang, J. Q., Baugh, A. T., Chapter 2 Glucocorticoid-Mediated Phenotypes in Vertebrates: Multilevel Variation and Evolution, p. 41-115, Copyright (2016), with permission from Elsevier.

An increase in circulating GC concentrations causes a suite of behavioural and physiological responses, such as increased production of glucose (Nelson, 2005) and a decrease in its cellular uptake by stimulating the production of a protein that removes glucose carriers from the cell membrane (Horner et al., 1987). The resulting increase in available energy can be observed about 80-100 minutes later (Munck and Koritz, 1962), which highlights the importance of GCs in the context of recovery rather than in the acute stress response (Sapolsky et al., 2000; MacDougall-Shackleton et al., 2019). Besides energy mobilisation, increases in GC concentrations have adaptive, pleiotropic effects in relation to an aversive stimulus; these include increased oxygen intake, inhibition of energetically demanding processes such as growth, digestion, immune function, and reproduction, decreased pain perception, and enhanced sensory functions and memory formation (Nelson, 2005). To have these multiple effects, GCs bind to different kinds of receptors, such as intracellular glucocorticoid receptors and mineralocorticoid receptors, which as dimers act as transcription factors with both suppressive and promotive effects (reviewed in MacDougall-Shackleton et al., 2019), as well as membrane receptors, which have multiple rapid effects, for example modulation of hormone secretion and neuronal excitability (Borski, 2000). Overall, GCs clearly play an important role in the physiological stress response and its recovery, as well as daily maintenance. GC metabolites can be measured non-invasively in wild vertebrates from urine (uGCM) or faeces (fGCM) and provide a well-established measure of physiological stress in the sense of metabolic demands, and as such fGCM concentrations will be utilised in this thesis.

It should be kept in mind that GCs only represent one small part of the neuroendocrine system and function as such in a complex interplay with neuronal systems and other hormones, such as testosterone and oxytocin (Uvnäs-Moberg, 1998). In particular, oxytocin, a neuropeptide and hormone, might play an important role in mitigating physiological stress responses, as it has been shown to inhibit stress-induced activation of the HPA-axis (Smith and Wang, 2014) and to be a central regulator of social attachment and other pro-social behaviour in animal studies (Romero et al., 2014). This way, it provides one potential pathway for the 'social buffering' effect, an effect that will be further described in section 1.2. While it would have been very interesting to investigate oxytocin concentrations in addition to GC levels, this was not possible in the context of this study due to practical issues with urine sampling.

1.1.2 The concepts of stress and stress reactivity

The concept of stress was introduced about a hundred years ago (Cannon, 1915; Selye, 1936) and entails three different parts: (i) the stressor, which is an unpredictable or uncontrollable stimulus that threatens homeostasis, (ii) the general stress response, which includes both the behavioural and physiological responses to this stimulus, and (iii) chronic stress, which describes the pathological consequences of long-term, unmediated stress (Romero et al., 2009). Stress is thus not only defined by arousal, which might be measured by physiological mediators, but also by the individual's perception of the situation being aversive and uncontrollable (Kim and Diamond, 2002). Homeostasis is defined as the maintenance of physiological parameters within normal ranges, e.g. of blood glucose levels (Romero et al., 2009). Allostasis is the concept of maintaining stability through change, i.e. the physiological mechanisms that maintain homeostasis via allostatic mediators (Romero et al., 2009). The allostasis model, however, focuses mainly on energy balances and has been criticised as being inadequate for fully explaining modulations of systems, such as behaviour, linked to early life experiences for example (Howell and Sanchez, 2011). Recently, a new model has been proposed, which builds on the allostasis idea and which has been termed the reactive scope model (Romero et al., 2009). This model allows the description of changes in mediator in response to predictable changes in the environment as well as unpredictable stimuli, and the consequences if these changes are substantial, frequent or long-lasting (Romero, 2012). The 'normal reactive scope' describes the range of mediator concentrations that entails the predictable variation of the mediator, e.g. circadian or seasonal variation, as well as the variation in mediator in response to unpredictable stimuli, i.e. stressors (Romero et al., 2009). Additionally, the reactive scope model enables modelling of ‘wear and tear’, which is the idea that there is a cost connected to higher levels of mediator, whether they are fluctuating in response to challenges or maintained at a raised level (Romero et al., 2009). More details on the reactive scope and the related demonstrated reactive scope models, on which this thesis is based, will be given in section 1.1.3.

Stress reactivity, in contrast to ‘stress’, describes the strength of the mounted physiological stress response, for example the increase in GCs due to the activation of the HPA-axis. In general, reactivity is defined as the “deviation of a physiological response parameter(s) from a comparison or control value that results from an individual’s response to a discrete, environmental stimulus” (Matthews, 1986). As such, a stress response that is appropriate for the stimulus is important to successfully cope with the challenge, i.e. stress reactivity that is too low would hinder the individual from successfully dealing with the stimulus, while stress reactivity that is too high would increase the negative effects linked to wear and tear. Additionally, a quick and efficient termination via negative feedback systems, for example, is necessary to avoid prolonged increases of GCs or other mediators, as these prolonged responses increase wear and tear (Romero et al., 2009; Taff et al., 2018). In addition to prolonged duration, a high frequency of activation of the physiological stress response system can also have effects on the system itself, in that it might lead to increased mediator baseline levels and worse recovery after subsequent stressor experiences (Taff et al., 2018). While stress reactivity is clearly a useful measure in the investigation of stress responses and their consequences, until recently there was no way of investigating it non-invasively. Studies in wild animals so far have measured stress responses invasively via serum samples to assess both baseline and stress-induced levels of GCs in response to capture and handling (e.g. in birds [snow buntings (*Plectrophenax nivalis*) and Lapland longspurs (*Calcarius lapponicus*); Wingfield et al., 1994], and in olive baboons [*Papio anubis*; Sapolsky, 1982]), or have used an ACTH challenge to assess maximal adrenal capacity (Romero and Wingfield, 2015). However, increases in mediator measured during capture and handling might not necessarily reflect the naturally occurring range of mediator, and invasive measures, especially in non-human primate species, are problematic due to their impact on the animal. Here, based on the reactive scope model, 'demonstrated reactive scope' provides a non-invasive measure of reactivity by reflecting the range of mediator an individual uses over a specific time period (MacLarnon et al., 2015). Thus, this study will use demonstrated reactive scope as a proxy for stress reactivity and the concept and metric will be further discussed in section 1.1.3 below.

1.1.3 The reactive scope model and demonstrated reactive scope

As described above, this thesis uses the demonstrated reactive scope, which is based on the reactive scope model, as a measure of stress reactivity. The reactive scope model (Romero et al., 2009) entails four ranges (see Figure 1.2 A): (1) predictive homeostasis, which covers for example circadian and seasonal variation in the physiological mediator; (2) reactive homeostasis, which is the range of the mediator needed to respond to unpredictable or threatening environmental changes. These two ranges together represent the normal reactive scope of the mediator; (3) homeostatic overload, which describes levels of the mediator above the reactive homeostasis, where, if the mediator reaches this range, it will lead to pathological problems; and (4) homeostatic failure, which is the range below the predictive homeostasis and which is incompatible with short-term health, as it makes coping with stressors impossible

(Romero et al., 2009).

As mentioned above, the reactive scope model also allows modelling of 'wear and tear'. Wear and tear (or allostatic load) can be understood as cumulative or sustained changes in mediator function, or as the ease with which the individual can keep its mediators in the reactive homeostasis range (Romero et al., 2009). Keeping mediators in this range is energy consuming and thus costly, so the costs increase the longer the mediator stays in the range or the more frequently it enters the reactive homeostasis range (Romero et al., 2009). Figure 1.2 B illustrates wear and tear as the progressive decrease in the threshold between reactive homeostasis and homeostatic overload, in response to repeated stressors that elicit short increases in mediator with a rapid recovery, represented by vertical lines (Romero et al., 2009). As in this scenario there is no acclimation to the repeated stressors, increases of the mediator of the same intensity enter the homeostatic overload range eventually, indicated by black vertical lines, and then start causing pathologies themselves (Romero et al., 2009). Once the stressors end, the previous threshold is recovered, but sustained changes in threshold and mediator function with longer term physiological consequences are possible (Romero et al., 2009).

Due to the difficulty of determining the normal reactive scope, the reactive scope model has only been used in a few studies in wild animals. For example, in Galápagos marine iguanas (*Amblyrhynchus cristatus*), efficacy of the negative feedback system modelled via the reactive scope model explained survival probability during famine (Romero, 2012). In house sparrows (*Passer domesticus*), experimental increase of allostatic load and thus a decrease in the remaining reactive homeostasis range were found to be linked to slower wound healing and stronger weight loss, after infliction of a wound (DuRant et al., 2016), and in male black redstarts (*Phoenicurus ochruros*), a species where males naturally do not show increased testosterone levels during territorial encounters, an artificial increase in testosterone within the individual's normal reactive scope did not affect the intensity nor persistence of territorial aggression (Goymann et al., 2015). The reactive scope model has also recently been used as a framework for the investigation of wild vervet monkeys' (*Chlorocebus pygerythrus*) fGCM concentrations in relation to environmental challenges such as droughts and low food availability, where it was observed that high levels of fGCM were associated with higher probability of mortality as predicted by the reactive scope model (Young et al., 2019).

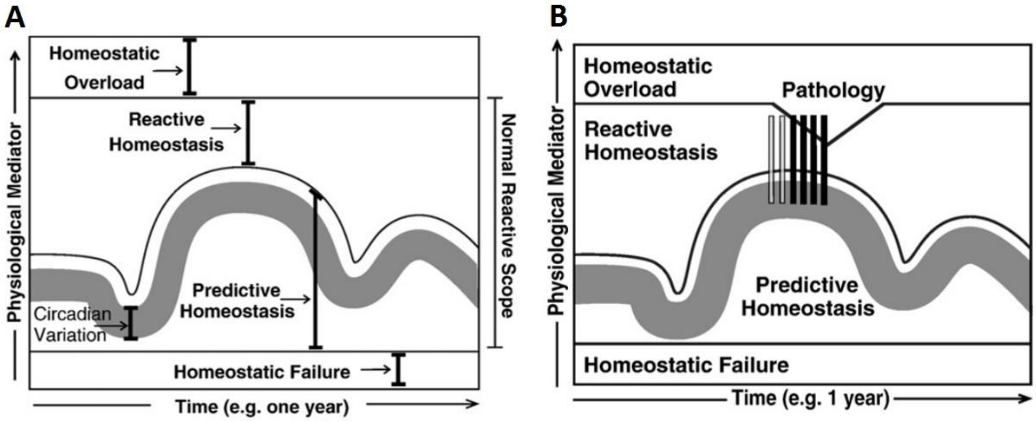


Figure 1.2 (A) The basic reactive scope model for a species living in a seasonally changing environment, as proposed by Romero, Dickens & Cyr (2009), illustrating the seasonal variation in predictive homeostasis, which includes circadian variation, and the reactive homeostasis range, into which the mediator goes in response to unpredictable stimuli (reflecting the general stress response); predictive and reactive homeostasis represent the normal reactive scope of the mediator. Below is the homeostatic failure range, which is incompatible with short-term health, and above the normal reactive scope is the homeostatic overload range, which is the level of mediator where the mediator itself will start to cause pathologies.
(B) Impact of repeated stressors on 'wear and tear', as represented by a progressive decrease in the threshold between reactive homeostasis and homeostatic overload. Vertical lines represent short physiological responses to the stressors with rapid recovery, and no acclimation to the stressors. As wear and tear increases, stress responses of the same intensity reach the homeostatic overload range (black lines) and thus start causing pathologies. In this model, the previous threshold is recovered after the stressors end, but long-term changes in the threshold caused by wear and tear is possible.
Reprinted from Hormones and Behavior, vol. 55, Romero, L. M., Dickens, M. J., Cyr, N. E., The Reactive Scope Model - a new model integrating homeostasis, allostasis, and stress, p. 375-389, Copyright (2009), with permission from Elsevier.

As described above, investigating the reactive scope model fully is not possible using non-invasive measures in wild animals, as it is only possible to determine the normal reactive scope of the measured mediator using invasive methods (Romero et al., 2009). Thus, a study on wild olive baboons (*Papio anubis*) developed a method for utilising the reactive scope model while using non-invasive data, which they called the demonstrated reactive scope model and which is graphically illustrated in Figure 1.3 (MacLarnon et al., 2015). Here, the measured range of an individual's physiological mediator X (e.g. GC concentrations assessed via fGCM) is termed the demonstrated reactive scope (DRS) and is calculated in percentage based on monthly averages as:

$$DRS_X = ((X_{max} – X_{min}) / X_{min}) \times 100$$

Additionally, the coefficient of variation (DRS_{CV}), which describes whether the mediator varies or is relatively stable (MacLarnon et al., 2015), provides a more stable measure than the DRS that is less affected by strong outliers, and is corrected for the number of months for which data is available (n):

$$DRScv_X = (\text{standard deviation}_X / \text{mean}_X) \times (1 + 4 / n)$$

As these are unit-free measures, this model allows a comparison between individuals or species in the range of reactive scope an individual or species utilises, independent of the matrix used, the individuals' body weight, or other individual or species-specific factors (MacLarnon et al., 2015).

In relation to the reactive scope model, the demonstrated reactive scope describes the range of mediator within the normal reactive scope the individual uses over a certain time period, and, as shown in Figure 1.3, this range might cover the total normal reactive scope, as illustrated for individual A, or part of the normal reactive scope, as indicated for individual B. For species living in their natural habitat, it is presumed that animals will adapt to the range of naturally occurring stressors encountered, and hence that the demonstrated reactive scope observed will be within the normal reactive scope (MacLarnon et al., 2015).

The non-invasive demonstrated reactive scope has been used in a few studies so far, for example to study thermoregulatory and dietary stress in wild olive baboons (*Papio anubis*; MacLarnon et al., 2015) and to study thyroid hormone levels in relation to thermoregulation in two different primate species (mantled howlers (*Alouatta palliata*) and Japanese macaques (*Macaca fuscata*); Thompson et al., 2017a). It has also been used to investigate personality in wild Barbary macaques (*Macaca sylvanus*; Tkaczynski et al., 2019) and been linked to rank differences in wild male rhesus macaques (*Macaca mulatta*; Zhang et al., 2018). Thus, using demonstrated reactive scope in addition to mean fGCM concentrations, this current study will provide on the one hand data of demonstrated reactive scope in a new species, which could later be compared to the other species due to the unit-free nature of the metric, and will on the other hand provide a comparison of different physiological stress response measures by studying simultaneously mean physiological stress response levels and stress reactivity.

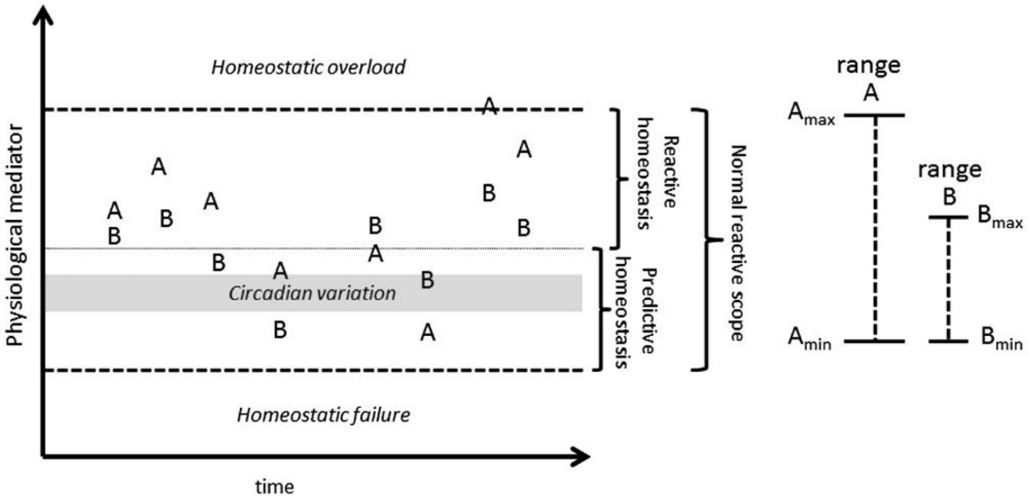


Figure 1.3 The reactive scope model (after Romero et al., 2009) for organisms in an environment with low or no seasonal variation. There are two sets of data, A and B, and their range of physiological mediator shown over a specific time period; A and B could be two individuals, but also troops, species etc. Indicated are the predictive homeostasis range, including circadian variation and other variation in response to predictable stimuli, and increases of mediator into the reactive homeostasis range in response to unpredictable stimuli, which together make up the normal reactive scope. Within the normal reactive scope, individuals experience wear and tear connected to higher levels of mediator, but no pathological consequences. Below the normal reactive scope is the range of homeostatic failure, and above the range of homeostatic overload; if mediator levels enter the homeostatic overload range in response to stimuli, this may result in pathological effects. Regarding the exemplary data, individual A experiences a greater range of the physiological mediator, and thus has a larger demonstrated reactive scope, than individual B, which reflects the greater wear and tear experienced by individual A. Reprinted from General and Comparative Endocrinology, vol. 215, MacLarnon, A. M., Sommer, V., Goffe, A. S., Higham, J. P., Lodge, E., Tkaczynski, P. J., Ross, C., Assessing adaptability and reactive scope: introducing a new measure and illustrating its use through a case study of environmental stress in forest-living baboons, p. 10-24, Copyright (2015), with permission from Elsevier.

1.2 Coping

While the physiological stress response, one part of which is the activation of the HPA-axis, enables animals to cope with perturbations and as such enables the individual for example to fight or flee, there are also ways in which the individual might be able to affect their physiological stress response levels. One of these is behavioural coping. The term coping generally means dealing with something challenging in an effective way (Lexico, 2019). Behavioural responses to a stressor have been termed coping behaviours, based on the ‘transactional theory of stress and coping’ in humans by Lazarus (1966), while Mowrer and Viek (1948) and Weiss (1968) conducted early important work linking coping behaviour to stress physiology in rats (*Rattus norvegicus domestica*).

Coping behaviour has often been defined as a behavioural response to an aversive situation that aims at removing the aversive stimulus if it is removable, or at least attenuating the physiological effects caused by the stressor (Wechsler, 1995). This way, the behavioural response plays a role in reducing the effect of the aversive stimulus on fitness directly, or on physiological measures that are related to fitness. As such, ‘successful’ coping behaviour, i.e. behaviour that removes the aversive stimulus and restores, or prevents a cost to, fitness, or that reduces the physiological consequences of the stress response, would have been under selection during the course of evolution, and coping behaviour is therefore believed to be an adaptive response to stressors (Wechsler, 1995). Early studies from Weiss (1968), for example, found that rats (*Rattus norvegicus domestica*) that were allowed to perform coping behaviours that controlled the tail-shocks they received suffered significantly fewer physiological symptoms of stress compared to animals that received the same level of shocks but were not allowed to perform the behaviour. Coping behaviour in the context of this study will thus be defined as any behavioural response to stressors which can be assumed to play a role in mitigating the animal’s stress response.

Coping behaviour, however, may not always be successful or fully successful, and should therefore not be defined by its success in removing the aversive stimulus (Wechsler, 1995). Animals, both in captivity and in the wild, sometimes fail to avoid or remove aversive stimuli, either because they have limited control over their environment or because, in the case of group-living animals experiencing social conflict for example, the benefits of group-living might outweigh the negative effects of conflict. Additionally, studies on rats (*Rattus norvegicus domestica*) have found that when considering the ‘success’ of coping behaviour, it is important to view separately the physiological and the behavioural consequences of stress: rats that received tail-shocks and showed active coping behaviour showed less anxiety-like behaviours in subsequent test situations than animals that did not perform coping behaviour, but coping behaviour did not alter the physiological response to tail-shock (Helmreich et al., 2012).

For a species-independent classification of coping behaviour, Wechsler (1995) suggested classifying coping behaviours into four coping strategies: here, animals could escape an aversive stimulus by (i) distancing themselves from the situation; (ii) removing the aversive stimulus by being aggressive; (iii) showing search and appetitive behaviour if a stimulus is absent and they can't fulfil their specific need, such as the absence of food or water; (iv) showing waiting or apathetic behaviour if they cannot remove or escape from the stimulus and can only conserve energy by waiting for a spontaneous change in the environment (Wechsler, 1995). The last strategy is sometimes transferred from one situation to the next, even if the environment might be different and the new stressor might be removable, and has then been termed 'learned helplessness' (Wechsler, 1995).

Based on the definition of coping behaviour given above, Gustison et al. (2012) summarised three main potential coping behaviours in non-human primates. Here, individuals might show aggression towards the aversive stimulus or a third-party, they might use affiliation as a way to mitigate the physiological consequences of the stress response, or they could show self-directed behaviour as displacement behaviour (Gustison et al., 2012). Previous research on these three areas of behaviour will be described in detail in chapter 4. Overall, though, coping behaviours have rarely been studied in wild non-human primate species, even though they might play an important role in individuals' ability to cope with everyday or extreme aversive situations. While Engh et al. (2006a) showed that wild female chacma baboons (*Papio ursinus*) increased their grooming in response to the loss of a relative in the subsequent month, and several studies found increased rates of displacement behaviours in anxiety-inducing situations such as proximity of a dominant individual (e.g. Barbary macaques [*Macaca sylvanus*; Paschek et al., 2019]; olive baboons [*Papio anubis*; Castles et al., 1999]), only one study in semi-free ranging Barbary macaques has experimentally investigated short-term changes in behaviour in response to a stressor (Gustison et al., 2012). The current study will explore for the first time the use of different potential coping behaviours in the short term, in response to potentially stressful experiences in a wild non-human primate species.

1.3 Social buffering

In addition to coping behaviours that are shown in response to a stressor, social bonds, and the presence of conspecifics more generally, have been suggested to attenuate the physiological stress response in aversive situations. The finding that the presence of a conspecific can lead to a quicker recovery after a stress response has been termed 'social buffering' (Kikusui et al., 2006) and shown to exist in many species, such as guinea pigs (*Cavia porcellus*; Hennessy et al., 2000), squirrel monkeys (*Saimiri sciureus;* Vogt et al., 1981), and humans (Thorsteinsson et al., 1998). In the short-term, social buffering can mitigate the HPA-axis activation in response to a stressor: in squirrel monkeys, for example, exposure to a live snake led to an increase in GC concentrations in response to this potential predator; if the individual was with their social group, however, no such increase was observed (Levine, 2000).

In the longer term, sociability has been linked to attenuated stress responses and fitness benefits. There are two key hypotheses potentially explaining this link: the social buffering hypothesis, i.e. beneficial effects of bonded partners only occur in stressful situations, and the main effect hypothesis, i.e. the beneficial effects of bonds occur in everyday life (Wittig et al., 2016). Wittig et al. (2016) investigated these two hypotheses in wild chimpanzees (*Pan troglodytes schweinfurthii*). They found that chimpanzees had lower urinary glucocorticoid metabolite (uGCM) concentrations in aversive, neutral, and positive contexts when they were in proximity to a bonded individual compared to the presence of non-bonded individuals, thus supporting the main-effect hypothesis of social bonds (Wittig et al., 2016).

In baboons, and other non-human primate species, having strong social bonds has been clearly linked to fitness benefits, such as enhanced infant survival (yellow baboons [*Papio cynocephalus*; Silk et al., 2003]; chacma baboons [*Papio ursinus*; Silk et al., 2009]), higher birth-rates (chacma baboons, McFarland et al., 2017), and a longer lifespan (yellow baboons, Silk et al., 2010b; Archie et al., 2014; rhesus macaques [*Macaca mulatta*; Ellis et al., 2019]). In males, social bonds have also been linked to increased reproductive success in Assamese macaques (*Macaca assamensis*; Schülke et al., 2010). Additionally, position in a social network has been shown to be predictive of some of the same fitness benefits, for example infant survival in chacma baboons (Cheney et al., 2016).

Even though the fitness benefits of social bonds have been repeatedly shown in baboons, few studies have linked social bonds to GC concentrations in baboons (as will be described in more detail in chapter 4). In female Assamese macaques (*Macaca assamensis*), being sociable with either males or females, i.e. spending time in close proximity and grooming them, was shown to be associated with lower levels of fGCM depending on the season (Fürtbauer et al., 2014). Only one study, to my knowledge, has linked social bonds specifically to GC levels in female chacma baboons (*Papio ursinus*), finding that 'loner' females had weaker bonds, unstable partner preferences, and higher GC concentrations than other females (Seyfarth et al., 2012). Otherwise, changes in affiliative social networks, assessed for example via grooming diversity indices, grooming partners, or time spent grooming, have been linked to GC concentrations in a few studies in chacma baboons (e.g. Crockford et al., 2008; Wittig et al., 2008). Therefore, investigating the association between social bonds and GC levels in chacma baboons might indicate one potential mechanism by which strong social bonds are linked to fitness benefits. Thus, this study will also explore the links between sociability (expressed via strong social bonds or social integration, the latter assessed using social network analysis) and GC levels in this wild baboon population, as will be discussed in chapter 4.

1.4 Resilience

Individuals differ in their ability to cope with stress and adversity. Resilience and vulnerability, which are two sides of the same concept, have been studied for a long time, both in animal sciences and psychological/psychiatric studies in humans (for example see Rutter, 1987). However, in many publications their definition or measurement remain unclear, and this is especially so in studies of animal behaviour. This might in part be due to the origin of the concept of resilience, as emotional or psychological resilience is one of the cornerstones of psychiatric thinking regarding responses to trauma (Karatsoreos and McEwen, 2011) and the concept originates from the finding of huge heterogeneity in response to different kinds of physical and psychological hazards observed in humans (Rutter, 1987). Therefore, in this section I will first define the term resilience as it will be used in the context of this study and then explain the 'three-hit concept' as a framework for the study of resilience. Specific examples of studies on resilience in non-human primates and other animal species will be given in chapter 5, where resilience and its link to demographic, behavioural, and social factors will be explored.

Definition of resilience

Resilience is a widely used term, but, even in psychological studies, resilience is conceptualised in many different ways and there are even discrepancies in whether resilience is defined as a trait, process, or outcome (Fletcher and Sarkar, 2013). In the context of this thesis, I will use Rutter's (2012) definition from psychological studies, where resilience is defined as "reduced vulnerability to environmental risk experiences, the overcoming of a stress or adversity or a relatively good outcome despite risk experiences". Resilience is here understood as a process rather than a fixed trait, where the ability to cope with adversity at one point in life does not necessarily correlate with the ability to cope with adversity at a different stage in life: "If circumstances change, resilience alters" (Rutter, 1987). Thus, resilience here is not understood as a personality trait as it can change with changing circumstances or changes in life-history stage. This also means that protective- or vulnerability-effects only become apparent in combination with a risk factor, and can thus also only be measured in the individual's response when faced with adversity; factors that have protective- or vulnerability-effects are not inherently positive or negative traits (Rutter, 1987). To be able to utilise the concept of resilience in the context of this study, I will primarily focus on the latter part of the definition: "a relatively good outcome despite risk experiences" (Rutter, 2012), i.e. I will compare individuals' success in dealing with everyday stressors to their conspecifics' success and put this in relation to the range of mediator they needed to utilise to cope with the experienced challenges.

To explore resilience based on the first half of the definition ("reduced vulnerability to environmental risk experiences, the overcoming of a stress or adversity"; Rutter, 2012) one would need to conduct a laboratory study where it is possible to control environmental factors which might influence resilience and investigate individual responses to single adverse events. Studying resilience in the wild, though, allows an investigation of the concept within an ecologically and evolutionarily relevant context. As such, the individual differences in resilience and vulnerability observed in the wild have evolved under natural selection pressures and are therefore meaningful in the investigation of inter-individual differences in fitness. Additionally, the degree of variation between individuals might differ between habitats or species, so studying variation in resilience in the wild might enable later comparisons of the degrees of inter-individual variation between populations.

Concepts of resilience

The three-hit concept (Daskalakis et al., 2013) provides a comprehensive framework with which it is possible to investigate different aspects of resilience and vulnerability. In this concept, genetic factors (hit-1) interact with environmental factors early in life (hit-2), leading to changes in the endocrine system as well as epigenetic modifications. This programs gene expression patterns in the developing brain, that are relevant for the phenotype. The resulting phenotype is then exposed to environmental factors later in life (hit-3). In combination with a certain environment, an individual human might be more vulnerable and at higher risk to develop psychiatric symptoms, while in a different environment this same individual might be more resilient (Daskalakis et al., 2013). Thus, even when individuals reach adulthood, their resilience is not a stable trait (and thus resilience should not be considered a personality trait) but might change depending on their current environment and their life-history stage.

This framework incorporates several hypotheses regarding early-life stress effects on resilience. The *cumulative stress hypothesis*, for example, proposes that vulnerability increases when failures to cope with adversities accumulate over time, either early- or later-on in life (Daskalakis et al., 2013). Other hypotheses are based on the finding that early-life experiences can lead to epigenetic changes which form the basis of predictive adaptive responses. Thus, the *predictive adaptive response hypothesis* proposes that these changes might prepare the individual for the predicted environmental or somatic conditions it will experience later-on (Lea et al., 2015; Berghänel et al., 2016), as will be discussed further in chapter 5. Should it come to a mismatch of adaptive phenotypic response and actual experienced environment, this is thought to increase the risk of disease (*developmental match/mismatch hypothesis*) (Daskalakis et al., 2013). Consistent with the match/mismatch hypothesis is the view that certain genetic predispositions, such as high reactivity to environmental stressors, might provide an adaptive benefit in one context, but lead to higher susceptibility in another (Belsky and Beaver, 2011). Individuals that are more reactive (to the environment) will be more susceptible to adverse situations but also potentially more sensitive to beneficial stimuli, while less reactive individuals may not react as strongly to any kind of environmental stimulus (*for better or for worse model*) (Daskalakis et al., 2013). Epigenetic and neuroendocrine modifications also form the basis of the *inoculation theory*, where a moderately stressful experience early in life leads to higher resilience to bigger challenges later-on in life, also called *steeling effects* (Rutter, 2012; Daskalakis et al., 2013). Severe stress in early life, on the other hand, may not have this effect but may enhance the risk of disease later-on. Similarly, the *developmental constraint hypothesis* proposes that low quality early-life environments are connected to lower adult fitness, in that individuals who experience a higher quality of environment early in life will always have a fitness benefit compared to individuals who experience a lower quality of early-life environment (Lea et al., 2015). One idea regarding these early life effects in a psychological context is also that successful coping with a challenge might promote positive outlooks linked to feelings of self-efficacy, which in turn might be an important part of subsequent resilience (Rutter, 2012). While it is uncertain if non-human primates experience emotions such as self-efficacy or positive outlook, coping has been shown to be linked to hippocampal neurogenesis in adult squirrel monkeys (Lyons et al., 2010), suggesting that successful coping can lead to neuronal changes even in adulthood.

Importantly, even though the terms (psychological) resilience and coping are often used interchangeably, these are two distinct concepts. In psychology, resilience determines how an event is appraised, whereas coping refers to the strategies utilised after the appraisal of the event (Fletcher and Sarkar, 2013). Thus, an individual might use a variety of different coping strategies or behaviours with varying effectiveness in dealing with the issue, while resilience would be connected to all stages of the stress response process, such as the initial appraisal, the meta-cognition regarding the first appraisal, as well as the choice of coping strategies (Fletcher and Sarkar, 2013). In studying resilience in animals, it is difficult to ascertain their appraisal of a situation or the existence of meta-cognition, but it is indeed possible to observe coping behaviours as mediators of resilience, as well as the outcome of this process as a proxy for resilience.

Based on this framework, this study aims to investigate inter-individual differences in resilience. Members of a baboon troop will have had different experiences in their infancy and adolescence, and these will have interacted with genetic predispositions. Based on the environment they live in today, which will to some degree differ between individuals, they are thus expected to show differential resilience in the face of adverse situations. While many factors, such as genes, pre- or post-natal modulation, early-life experiences, or current life-history factors, might mediate and contribute to an individual's resilience, I will focus in this thesis on socially and behaviourally mediated resilience. This approach follows from the idea that sociability and/or behaviour link to individuals' experience of stress and their ability to cope with it, for example via coping behaviour, strong social bonds, or social buffering. These might in turn be influenced by different kinds of early-life experiences or predisposition, but those cannot be covered in the context of this thesis.

1.5 Overall aims of this study

As described above, there are many gaps in our knowledge of how and why individuals differ in their resilience to stressful experiences. This study aims to fill some of these gaps in our knowledge regarding resilience in wild animals, by investigating the different steps in the process of resilience using chacma baboons (*Papio ursinus*) as a model species. Chacma baboons are an ideal study species, as they live in large multi-male multi-female troops (Hamilton et al., 1976), which provides substantial inter-individual variation in sociability, stress, and fitness, are relatively long-lived (Cheney et al., 2004), and have been intensely studied regarding their social behaviour and fitness, as described above. Figure 1.4 shows the process of resilience simplified and exemplified for one stressor, indicating the steps which are described in each chapter. Based on this process, this study aims to answer the following main research questions:

Do mean physiological stress response levels and stress reactivity differ between demographic groups, i.e. depending on sex, age, reproductive state, and dominance rank position, and are physiological stress response measures linked to environmental factors, such as climate or predation? (chapter 3)

Do chacma baboons use coping behaviours in response to aversive situations and are these linked to physiological stress response measures in the short- or long-term? (chapter 4)

Are social bonds or social integration connected with lower mean physiological stress response levels or stress reactivity, reflecting social buffering? (chapter 4)

Is it possible to measure resilience non-invasively using relative measures of success and stress reactivity, and is resilience socially or behaviourally mediated in chacma baboons? (chapter 5)

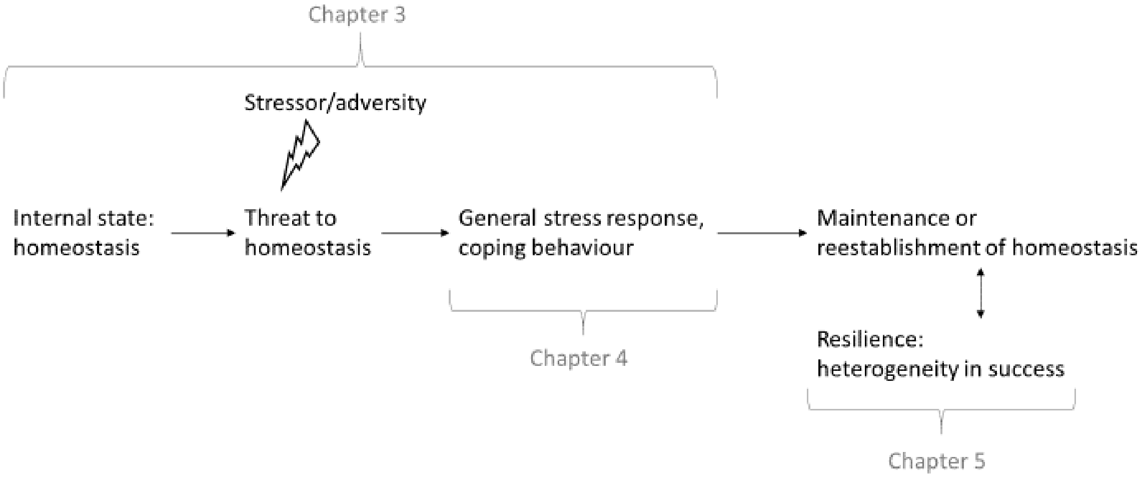


Figure 1.4: Simplified process of resilience in coping with one stressor or adversity, from homeostasis before the stressor, to the general stress response and potential coping behaviours in response to the stressor, and finally the reestablishment of homeostasis and the measurement of resilience as relative success. The chapters in which these stages are discussed are indicated.

1.6 Terminology

In the context of stress and resilience, certain terms have been used ambiguously or simplistically in the literature. For example, GCs have often been termed the 'stress hormone', even though they mediate energy mobilisation via the regulation of carbohydrate metabolism more generally (MacDougall-Shackleton et al., 2019). To avoid unclear interpretations in this study, I will therefore use the following definitions and terms:

Stressor: a real or perceived threat to homeostasis, that elicits a physiological stress response, measurable as increased GC concentrations reflective of the increased energetic demands; other synonymous terms used: adverse or aversive situation or stimulus, challenge, perturbation

Physiological stress response measures: any measures of fGCM concentrations or variations used in this study

Mean physiological stress response levels: measured as mean fGCM concentration for an individual, as a proxy for the longer-term energy expenditure; as such includes both baseline and peak concentrations

Stress reactivity: the strength of the physiological response to a stressor; here, described by measures of demonstrated reactive scope (DRS and DRS_{CV}) of fGCM as non-invasive indicators of long-term reactivity

Coping behaviour: a behaviour shown in response to a stressor, that serves to remove the stimulus or attenuate the negative effects of the physiological stress response

Resilience: a process of coping with an adverse situation ending in a relatively good outcome despite the risk experience

2. General methods

2.1 General information

2.1.1 Study species – chacma baboons

2.1.1.1 Species, subspecies, range

This study was conducted on southern chacma baboons (*Papio ursinus ursinus*) (Kerr 1792). Baboons are part of the family of 'Old World Monkeys' (Cercopithecidae), which is distributed across Africa and Asia. Chacma baboons are one of the five currently recognised species of the genus *Papio*, which also includes *P. anubis* (Lesson 1827), the olive baboon; *P. cynocephalus* (Linnaeus 1766), the yellow baboon; *P. hamadryas* (Linnaeus 1758), the hamadryas baboon; and the Guinea baboon, *P. papio* (Desmarest 1820). Baboons occur in most parts of sub-Saharan Africa – from Mali in the north to the southern end of South Africa, and from Senegal to Ethiopia and Somalia – as well as in the Arabian Peninsula (Wilson and Reeder, 2005).

There are two recognised subspecies of chacma baboons, with *P. ursinus griseipes* (grey-footed chacma baboon - Pocock 1911) ranging from south-west Zambia over the Okavango Delta in Botswana, to Zimbabwe and Mozambique (south of the Zambesi), and *P. ursinus ursinus* (southern chacma baboon - Kerr 1792) occurring in the remainder of the range, i.e. throughout Namibia and in all provinces of South Africa (Grubb et al., 2003; Groves, 2005; Hoffmann and Hilton-Taylor, 2008) (see Figure 2.1). Groves (2005) recognises a third subspecies, *Papio ursinus ruacana* (Shortridge 1942), occurring in northern Namibia and Angola, which Grubb (2003) questions as a distinct subspecies and suggests considering it as part of *P. u. ursinus*. Chacma baboons are listed as 'least concern' on the Red List of the IUCN as they are abundant and are not considered to be facing any major threats that might lead to range-wide declines (Hoffmann and Hilton-Taylor, 2008). In the context of this thesis, the study animals are referred to as chacma baboons or simply baboons.

Figure 2.1 Range of both subspecies of chacma baboons (*Papio ursinus*) across southern Africa (yellow shaded area) (Sithaldeen, 2019, IUCN [International Union for Conservation and Nature] accessed March 2020).

2.1.1.2 Group living, life-history stages

Chacma baboons live in relatively large, permanent multi-male and multi-female troops of 4 to about 130 individuals (Hamilton et al., 1976; Hill and Lee, 1998). While most males disperse, females are philopatric with hierarchies following matrilines (i.e. kin-based subgroups) (Silk et al., 2009). The species shows distinct sexual dimorphism, with males (about 28 kg) weighing about twice as much as females (about 14 kg) (Mitani et al., 1996).

Males are considered to reach maturity at around 8 to 9 years of age (Bergman et al., 2005), at which time they have fully developed shoulder musculature, large testes and long canine teeth (Weingrill et al., 2003). Once they reach maturity, most males disperse and join other troops, either without ever challenging the hierarchy of their natal troop or after rising in the ranks and eventually being defeated; some males, however, never leave their natal troop (Kitchen et al., 2003). Males tend to form a transitive, linear dominance hierarchy, which is often only stable over shorter periods of time, with tenure of the dominant male rarely lasting more than a year (Kitchen et al., 2003).

Cycling female baboons show sexual swellings that increase during the early follicular phase and reach their maximum size around the ovulatory period, in accordance with rising oestrogen levels, then decrease rapidly with the onset of the luteal phase, and as such they are indicators of receptivity (yellow baboons [*Papio cynocephalus*; Gesquiere et al., 2007]). The fertile period lasts about 5 days (olive baboons [*Papio anubis*; Higham et al., 2008]). During this period, males will compete to consort and mate with the receptive female, with high-ranking males able to monopolise fertile females during their most receptive days, whereas lower ranking or subadult males often consort females before or after their peak of receptivity (chacma baboons [*Papio ursinus*; Weingrill et al., 2003]). Gestation lasts on average 177 days (yellow baboons, Beehner et al., 2006) and infants are generally dependent on their mother for one year, with one of the youngest recorded infants surviving the loss of their mother being 9 months old (Cheney and Seyfarth, 2007). The inter-birth interval of chacma baboons ranges from 20 to 38 months and was found to depend on a combination of environmental and demographic factors (Hill et al., 2000). Similarly, depending on environmental factors, chacma baboons are non-seasonal breeders at some sites (Weingrill et al., 2004), while seasonal patterning has been observed at other sites (i.e. higher birth rates during wet than dry months in the Drakensberg mountains)

(Lycett et al., 1999). Females are considered adolescent when they develop their first sexual swelling, signalling menarche, at around 4 to 5 years of age (hamadryas baboons [*Papio hamadryas*; Bronikowski et al., 2002]), and are classified as adults once they have given birth to their first infant, normally at around 6 years of age (Altmann, 1980; Bergman et al., 2005; Engh et al., 2006b).

2.1.1.3 Habitats

Chacma baboons are adapted to living in varying types of habitat and can consequently colonise many kinds of woodland, steppe, savanna, subdesert and montane regions such as the Drakensberg mountains, as well as Cape Fynbos and Succulent Karoo (Hoffmann and Hilton-Taylor, 2008). Habitat choice is influenced by predation risk, available water sources, and availability of suitable sleeping sites, such as cliffs, hills, or tall trees, to avoid predation at night (Hamilton et al., 1976; Hoffmann and Hilton-Taylor, 2008). Baboons are opportunistic omnivores with a mainly plantbased diet made up of bulbs, shoots, roots, seeds or fruits, but they will also eat invertebrates and smaller vertebrates when available (Hoffmann and Hilton-Taylor, 2008). When the opportunity arises, baboons also prey on young of, or small bodied, antelope species (Hoffmann and Hilton-Taylor, 2008). As opportunists, baboons raid crop farms, plantations, and vineyards and as a result come into conflict with humans in settled areas, with people often retaliating by injuring or killing baboons (Hoffmann and Hilton-Taylor, 2008; Hoffman and O'Riain, 2011). Spatial conflict behaviour between troops of baboons depends on habitat, resource availability and subsequent home range sizes, and can vary from aggressively defended boundaries to widely overlapping home ranges with more tolerant intergroup encounters (Hamilton et al., 1976).

2.1.2 Study site

Data were collected at the field site of the Primate and Predator Project (University of Durham, UK) at Lajuma Research Centre (23°02′23″S, 29°26′05″E). The research centre is located in the western part of the Soutpansberg mountain range, Limpopo Province, in northern South Africa, and is situated in a mountainous region (altitudinal range on site: 1150-1750m) (Willems et al., 2009; see Figure 2.2). Due to the high biodiversity, the Soutpansberg mountains are part of the UNESCO Vhembe Biosphere Reserve (http://www.vhembebiosphere.org/about-vbr). Several studies have been conducted on the habituated troop of chacma baboons at this site (De-Raad, 2012; Howlett et al., 2015; Tomlin, 2016; Howlett and Hill, 2017), as well as on other primates at the site, such as Samango monkeys (*Cercopithecus albogularis schwarzi*; Coleman and Hill, 2014) and vervet monkeys (*Chlorocebus pygerythrus*; Willems et al., 2009).

Figure 2.2 Location of Lajuma Research Centre (tip of white arrow) in the Soutpansberg mountains (red area) in South Africa (from Willems, 2007).

2.1.2.1 Flora

The habitat at Lajuma is classified under the unique Soutpansberg mistbelt forest group and is as such covered by a mosaic of a diverse range of habitat types, such as Northern Mistbelt Forest, Soutpansberg Summit Sourveld, and Soutpansberg Mountain Bushveld (Mucina and Rutherford, 2006). Another study specific to the Soutpansberg Mountains and the Blouberg Mountains described 5 major vegetation types in the Soutpansberg Conservancy (Mostert et al., 2008), in which Lajuma is located and through which the baboons range. These are:

1. the Soutpansberg Arid Northern Bushveld: open woodland with a sparse field layer on the rain-shadowed north side of the ridge
2. the Soutpansberg Moist Mountain Thicket: low, closed thickets, made up of a layer of trees and shrub of 1.5-4m height, on the steep southern slopes
3. the Soutpansberg Leached Sandveld: relatively homogeneous group of woody and grass species with low species richness, occurring on the warmer northern slopes and arid southern slopes along the most northern ridges of the mountain range
4. the Soutpansberg Cool Mistbelt: occurs only above 1200 m above sea level and is confined to the mistbelt region with its frequent rains and mists, resulting in a high diversity of peatlands, low open grasslands and small islands of thickets and bush clumps
5. the Soutpansberg Forest (evergreen high forests in the mistbelt region and deciduous shrub forests on the southern slops of the southernmost ridges)

2.1.2.2 Fauna

Besides the richness of plant species, the Soutpansberg mountains also have a high biodiversity of insect, reptile, bird, and mammal species, with 60% of all animal species occurring in South Africa being found here (Gaigher and Stuart, 2003). In addition to chacma baboons, all of the other non-human primate species occurring in South Africa can be found in the Soutpansberg mountains, i.e. vervet monkeys (*Chlorocebus pygerythrus pygerythrus*), Samango monkeys (*Cercopithecus albogularis schwarzi*), lesser bushbabies (*Galago moholi*), and thick-tailed bushbabies (*Otolemur crassicaudatus*) (Tomlin, 2016).

There is also a range of carnivore species occurring at the site, including some that are known to predate on baboons, such as leopards (*Panthera pardus*), and some that could potentially predate on certain age-sex classes, such as brown hyaena (*Hyaena brunnea*), caracals (*Felis caracal*), and servals (*Lepatailurus serval*). Even though baboons at the site do not seem to adapt their habitat use to predation risk, in contrast to smaller non-human primate species there (Coleman and Hill, 2014), leopards do pose a constant predation threat; baboons were shown to make up 4.3% of leopards' diets at the site (Chase Grey, 2011). While the leopard density used to be especially high in the Soutpansberg mountains (Chase Grey et al., 2013) and has since undergone a steep decline (Williams et al., 2017), leopards still pose a strong predation threat to baboons at the site, and in the study period of this thesis two adult baboons were known to be killed by leopards (personal observation).

Besides carnivores, some larger species of birds of prey also pose a potential threat to young baboons at the site, with martial eagles (*Polemaetus bellicosus*), crowned eagles (*Stepahnoaetus coronatus*), and Verreaux's eagles (*Aquila verreauxi*) being confirmed there (De-Raad, 2012). However, no predation events by eagles were seen or suspected during data collection.

Several different snake species occurring at this site might also pose a threat to baboons, such as the African rock python (*Python sebae*), black mamba (*Dendroaspis polylepis*), Mozambican spitting cobra (*Naja mossambica*), puff adder (*Bittis arietans*), and boomslang (*Dispholidus typus*) (De-Raad, 2012). While no injuries or deaths confirmed to be caused by snakes occurred during the study period, several of these snakes were observed in the baboons' home range. Additionally, on several occasions, baboons detected snakes (as discernible from their behaviour), but the species could not be identified by the observers.

Besides this risk of predation, baboons also predate on other mammals if the opportunity arises. A few cases of baboons predating on vervet monkeys have been confirmed at the site (De-Raad, 2012), even though there were no confirmed cases during the study period. Additionally, baboons prey on smaller mammal species (e.g. hares), the young of antelope species, such as red duiker and bushbuck, and small birds. Several cases of predation on young antelope were observed during the study period, but identification of the prey species was not possible.

2.1.2.3 Climate

Climatic conditions at Lajuma are mesothermal, with cool and dry winters (May to August, temperatures ranging from 12-22°C) and warm and wet summers (December to February, temperatures ranging from 16-40°C), with an annual mean temperature of 17.1°C and an average annual rainfall of 724mm (Kabanda, 2003; Willems et al., 2009). The Soutpansberg mountain range lies in the summer rainfall zone of South Africa, and due to its east-west orientation experiences orographic rainfalls (Mostert et al., 2008).

The southern slope in particular (where Lajuma is located) experiences large amounts of rain and mist during the rainy season, while the mountain range causes a rain-shadow effect on the northern slopes (Mostert et al., 2008). Local weather data are constantly recorded at 30-minute intervals at the field site, using a Davis Instruments Vantage Pro II integrated sensor suite that is linked via WIFI to a console with data logger. Data are made available by the Ndlovu Node of the South African Environmental Observation Network (SAEON; www.saeon.ca.za) under the North-eastern Mountain Observation project; the station is maintained, and data are disseminated, by Lajuma Research Centre. The recorded data on mean temperature and rainfall during data collection (January to November 2017) are shown in Figure 2.3.

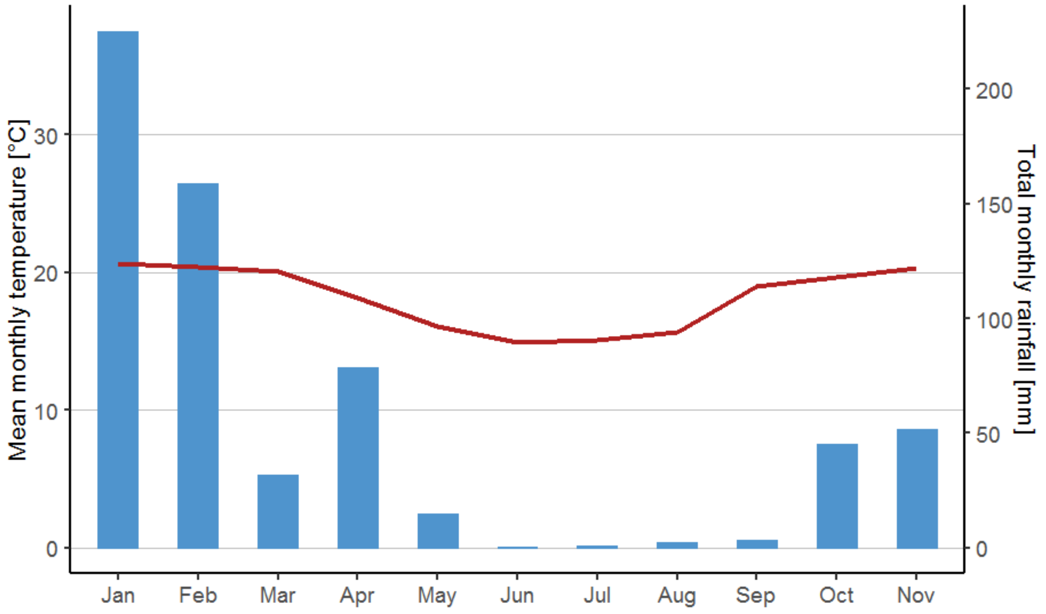


Figure 2.3 Weather data recorded at Lajuma Research Centre averaged per month over the study period (January to November 2017) with mean monthly temperature [°C] (red line) and total monthly rainfall [mm] (blue columns). Data are made available by the Ndlovu Node of the South African Environmental Observation Network (SAEON; www.saeon.ca.za) under the North-eastern Mountain Observation project.

2.2 Data collection

Data collection took place from January to November 2017, thus covering both the rainy season (December to March) and the dry season (April to November). Data were collected by three observers: the author of this study (ZM) and a field assistant working on this project (Allison Stitt; AS) collected behavioural data via continuous focal animal sampling, as well as via *ad libitum* sampling of dyadic agonistic interactions. ZM and AS also collected large part of faecal samples for hormone metabolite concentration analysis, as well as conducted coat condition ratings and took thermal imaging pictures for the assessment of coat insulation quality. ZM and AS also collected opportunistically data on wounds, sickness behaviour, and wound healing, as well as on matings, consortships, and reproduction during the data collection period. Another PhD student at the field site (Andrew Allan; AA) collected *ad libitum* data on dyadic agonistic interactions and added to the faecal sample collection. Longer-term data on reproduction and survival were provided by the Primate and Predator Project, to a large part collected by AA. Details of inter-observer reliability are given with the respective methods sections (i.e. regarding continuous focal animal sampling in section 2.2.2.2, and regarding coat condition ratings in section 2.2.4 of this chapter).

Observations were made on one wild group of chacma baboons, which although habituated to and often accompanied by humans, still faced naturally occurring stressors. These ranged from ecological stressors such as a drought period and predation events by leopards (described in more detail below), to more social stressors, such as immigrating males with subsequent potential risk of infanticide and periods of hierarchy instability. The troop also experienced some man-made stressors, firstly as a result of being chased away by farm workers while crop-raiding adjacent avocado and macadamia nut farms, and secondly during one period of trapping (lasting two weeks) during the study period. For this, corn as bait was spread around the trap, which led to high rates of aggression on site, and one adult female (together with an adolescent male) were trapped, with the female being anaesthetised and fitted with a GPS collar.

All data collection for this project was conducted following ethical approval by the University of Roehampton (Appendix I-II), the necessary local research permits are held by the Primate and Predator Project, and importation of faecal samples was done under the authorisation of the Department for Environment, Food and Rural Affairs (Appendix I-III).

2.2.1 Study subjects

2.2.1.1 Age classes

The study group of wild, habituated chacma baboons (*Papio ursinus)* numbered about 100 individuals. Animals were categorised into age classes at the beginning of the study. Females were considered to be adolescents when they reached menarche, which occurs between 4 and 5 years of age (Bronikowski et al., 2002), and to be adult once they gave birth to their first infant, which is normally around 6 years of age (Altmann, 1980). One adult female (sho) was obviously of adult age and was classified as such, even though she is believed never to have given birth. Males were considered adolescent once their testes descended and adult when they had fully developed shoulder musculature, large testes and long canines (Weingrill et al., 2003).

2.2.1.2 Group composition

At the start of data collection, the group consisted of 23 adult females, 6 adolescent females, 8 adult males, 4 adolescent males, and an unknown number of juveniles of different age ranges. Only adult females (one of which had to be excluded from the study as she was not habituated well enough, thus leaving 22 adult females) and adult and adolescent males (the latter as they were considered to be important interaction partners for the adult females, and some became involved in dominance interactions; following De-Raad, 2012) were included in the study (overall n=34). Adolescent females were excluded, partly due to their not being reliably identifiable and partly because of the number of juvenile females expected to transfer to the stage of adolescence during the study period. One adolescent female gave birth to her first infant near the end of the study period but was not included because of the short time left during which observation would have been possible.

Adult individuals were categorised as young, middle, or old-aged based on previous recordings and reproduction. For the females, individuals that had their first infant in 2014 or subsequent years were classified as young adults; if they were recorded as adult females in 2012/2013 as middle-aged; and if they were already adults in 2008 as old-aged. Thus, seven females were classified as young, seven as middle-aged, and six as old-aged (see Table 2.1). Regarding adult males, individuals were categorised as young adults if they only showed the physical characteristics of adulthood described above from 2016 onwards (or if they immigrated in 2016 when comparably small, e.g. bor and igo); as middle-aged if they immigrated before 2016 or immigrated as a fully-grown male in 2016 (e.g. nos); and as old adult if they had already been recorded as adult males in 2008. Of the males included, four were categorised as adolescent at the beginning of the study period, four as young adults, two as middle-aged, and two as old-aged adults (see Table 2.2).

Table 2.1 Adult females included in the study classified into age groups (young, middle, old AF; AF = adult female) based on previous recordings and reproduction data, sorted by age class.

Individual	Age Class	Comment
box	Young	Young AF in 2014
bru	Young	1st infant Dec 2016
fat	Young	1st infant Oct 2014
gru	Young	1st infant beginning 2015
pix	Young	1st infant Apr 2014
tri	Young	1st infant beginning 2014
tup	Young	Adolescent in 2012, 2 infants before current that did not survive
man	Middle	Young AF in 2012
mel	Middle	Young AF in 2012
nor	Middle	Young AF in 2012, 3 infants
sct	Middle	Has ca. 5-year-old off-spring
sil	Middle	Young AF in 2013
sli	Middle	Young AF in 2012
yol	Middle	Young AF in 2013
bra	Old	Old AF in 2008
ela	Old	Old AF in 2008
hea	Old	Old AF in 2012, 2 to 3 infants
lob	Old	Old AF in 2012, 3 to 4 infants
per	Old	Old AF, confirmed during trapping 2017; killed by leopard in July 2017
rip	Old	Old AF in 2008
sho	Old	AF in 2008; disappeared in Oct 2017
ste	Old	AF in 2008, at least 3 infants; disappeared in Oct 2017

Table 2.2 Males included in the study classified into age groups (adolescent, or young, middle and old AM; AM = adult male) based on previous recordings, sorted by age class.

Individual	Age class	Comment
cro	Adolescent	Adolescent
fla	Adolescent	Adolescent; emigrated in June
fle	Adolescent	Adolescent at beginning of study period
nat	Adolescent	Adolescent
blo	Young	Just became AM at beginning of study period
bor	Young	Immigrated in April 2016, smaller than nos at the time; killed by leopard in Nov 2017
gor	Young	AM since Aug 2016; emigrated in Sep 2017
igo	Young	Immigrated in April 2016, smaller than nos at the time
nos	Middle	Immigrated as big AM in April 2016
scf	Middle	Immigrated between 2011-2013
dav	Old	AM since 2008
jos	Old	Old AM in 2008

Missing individuals

During the study period, several individuals disappeared or were known to have been killed. In June, one adolescent male (fla) disappeared and was assumed to have emigrated, as he was seen on several occasions in the home range on his own, probably because there were no other troops nearby at the time. A second male (gor) disappeared, presumably having emigrated, in September and at least one infant and one juvenile are assumed to have followed him, as they were not seen again.

An adult female (per) was killed by a leopard while observers were with the troop in July, about two weeks after she had been trapped and fitted with a collar. Her youngest offspring was about one year old (thus considered juvenile) and survived the loss of the mother but disappeared together with the emigrating male (and infant) as described above. Two adult females disappeared over the course of two days in October. One of them (sho), who was very low ranking and nulliparous, was last seen walking away from the troop. The other female (ste) had lost her infant 2 weeks prior to her disappearance and had herself become separated from the troop the day before; therefore, even though she had shortly after re-joined the troop, it is assumed that she might have died of dehydration or exhaustion. An adult male was also preyed on by a leopard in the presence of observers in November. He had sustained a major injury at the beginning of the year, which had led to a loss of function of his left hind leg; he had just regained function of this limb a few weeks prior to being killed.

Infants

Eight females were carrying infants at the beginning of the study, another nine gave birth during the study period, leaving only five without dependent young at any point in the study. Of all these infants, two died or disappeared during the study period; one died due to injuries caused by an adult male, potentially the father (i.e. mishandling and carrying it for too long), the other one disappeared together with the adolescent male, potentially following him when he emigrated, as described above.

After the study period

Two more adult females disappeared for unknown reasons in November just after the end of the study period. One of them had a three-month-old dependent infant, which also disappeared, the other one's infant was about 11 months old at the time and is believed to have survived the loss of the mother. Another female's infant, also 11 months old, disappeared around the same time.

Matrilines

In general, female chacma baboons form linear dominance hierarchies along matrilines, i.e. female maternal kin most of the time occupy adjacent ranks, with mothers being higher in rank than their daughters and younger daughters outranking their older sisters (Silk et al., 1999). Maternal relations play an important role in structuring the social behaviour of female baboons, as females have been observed to selectively groom maternal kin (Silk et al., 1999), form vocal alliances with maternal kin (Wittig et al., 2007), and be more tolerant to kin than non-kin females (Silk et al., 2010a). Thus, matrilines might play an important role in the context of stress and resilience, in addition to being potentially closely linked to dominance rank position and genetic predisposition, both of which might also affect the physiological and behavioural stress response systems as well as resilience, as described elsewhere. However, as data on the study troop has only been collected consistently since 2013 and genetic data were not available, kinship between adult individuals is unknown. Additionally, no obvious matrilines or kinships were discernible during observations – as Figure 2.4 shows, females appeared to groom females of adjacent rank, which could potentially be maternal or paternal kin, but also groomed extensively across the dominance hierarchy, making it difficult to estimate matrilineal relations. Indeed, observing the seemingly random affiliative interaction patterns and finding no obvious likeness in physiognomy, it needs to be considered that, while there must obviously be female kin in the troop, the study group might deviate from the normally described patterns in that it might consist of many small groups of maternally related females and might thus not be strictly structured by several large matrilines, potentially linked to the way the group developed (possible scenarios include high predation pressure in the past or fission or fusion of troops).

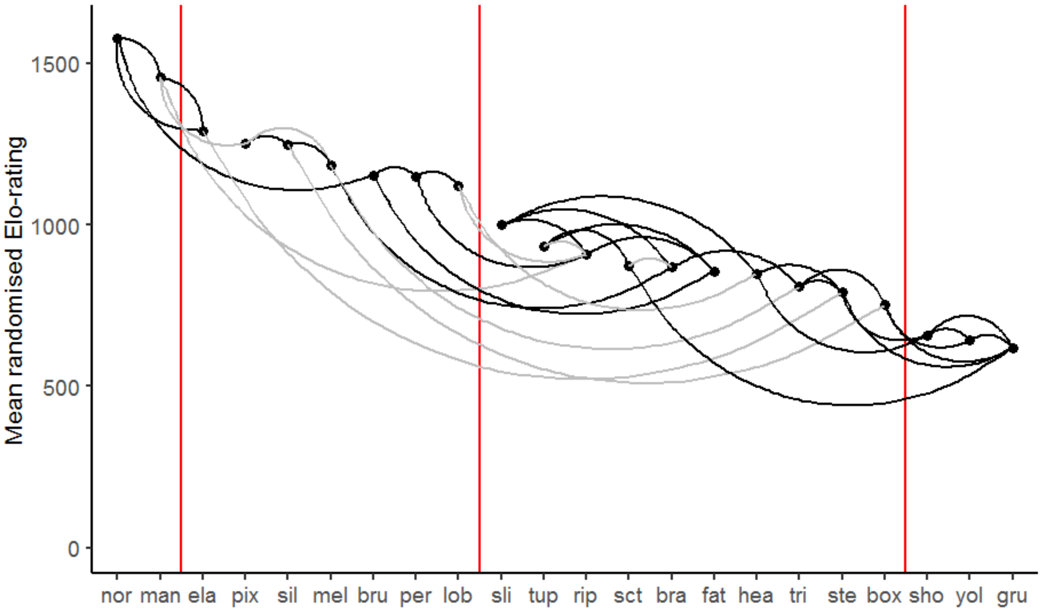


Figure 2.4 Females' grooming interactions by dominance rank positions. Females are noted on the x-axis sorted by their dominance rank position, starting with the highest-ranking female. The y-axis indicates the females' mean randomised Elo-ratings (procedure for calculation see section 2.2.2.2); red vertical lines indicate rank categories, as described in section 2.2.2.2. For each female, the three strongest grooming relations are indicated by curved lines, with grey lines reflecting relatively weak grooming relations (i.e. at a rate below 0.01 hours/focal hour), if these were still within the top three strongest relations of the female. Grooming relations were assessed using duration of grooming in hour/focal hour, including durations of both giving and receiving grooming during focal observations of either female and are thus undirected. Initially upwards curved lines indicate grooming relations between adjacent ranks or within rank categories, while grooming relations between females of different rank categories are depicted by initially downward curved lines.

2.2.2 Behavioural data

2.2.2.1 Data collection

Data were collected from the 6th of January to the 3rd of November 2017, using continuous focal and *ad libitum* data collection methods. At the beginning of each observation, the date, time of day, weather, reproductive status of the females, consortship status if applicable, and wounds or injuries were noted. Weather categories used were cloudy, cloudy & misty, mostly cloudy, partly cloudy, rainy, and sunny. Reproductive status of females was classified as cycling (no swelling, small swelling, medium swelling, or large swelling), pregnant or carrying an infant.

As behavioural strategies can change over the day (Sick et al., 2014), observations were balanced for each subject between different times of day, i.e. between morning (0600-1000), lunch time (1000-1400), and afternoon (1400-1800). For each observer it was assured that they observed each individual for a comparable amount of time. Individuals to be observed were split into two groups and assigned to an observer, who switched groups once every individual had been observed. Randomisation of observation order was attempted, but, due to the very difficult terrain, often focal animals were selected opportunistically (as done in Kalbitzer et al., 2015). Priority was given to individuals that had been less observed, either generally, at the specific time of day, or by the observer concerned.

Continuous focal observations

Data on social and self-directed behaviours were recorded using continuous focal animal sampling (Altmann, 1974). Durations of observation ranged from 2 to 37 minutes (mean 12.35 minutes), depending on how long an individual could be followed. General aim were 20 minutes focal observations, with longer observations only conducted if the individual lacked observation time; no observations shorter than 2 minutes were included. Overall, 317.54 hours of observations were recorded, ranging from 9.13 to 10.2 hours/individual, with the exception of individuals that disappeared during the study period which had substantially shorter overall hours of observation (i.e. 3.29, 4.56, 7.61, 8.09, and 8.13 hours/individual depending on time of disappearance).

Behaviours recorded included all social behaviours (i.e. agonistic and affiliative behaviours) from or directed towards the focal individual (agonistic behaviours based on Kitchen et al., 2003; Ellis et al., 2011), as well as all so-called “displacement” behaviours, which will be called self-directed behaviours in the context of this study (behaviours used based on Ellis et al., 2011). For females with dependent offspring, behaviours of other individuals towards the offspring were additionally recorded. For a description of all behaviours recorded, see Appendix II-I. Due to the very challenging habitat it was not possible to conduct parallel observations and statistically assess inter-observer reliability. However, at the beginning of, and at semi-regular intervals throughout the study period, the main investigator (ZM) observed the field assistant (AS) doing focal observations, thus assuring that behaviours were identified and recorded in the same way by both observers.

Durations of focal observations and general focal data collected were severely limited by challenging field work conditions – the terrain was very rocky and the dense bush that covers large parts of the home range consisted mostly of thorny shrubs, such as various Acacia species, so that observations had to be recorded vocally on Dictaphones, so as to not lose the focal individual, and then transcribed afterwards, which in turn limited the time spent with the baboons. During observations, observers frequently lost sight of the focal individual anyway due to the sometimes-impenetrable bush, rocky terrain, and swamps. Additionally, the mountain is made of terraces with steep cliffs in between, so that it was often impossible to directly follow the troop and it would take hours to find them again. All in all, due to these challenges, focal observations were sometimes - and especially in the beginning - short, and overall observation times are relatively low compared to other field sites, which should be taken into account when interpreting results.

Ad libitum sampling

During focal observation and between observations, data were also collected *ad libitum* on matings as well as on any dyadic agonistic interactions (Altmann, 1974). As the latter were used to calculate dominance hierarchy positions, only interactions with clear winner and loser were recorded, i.e. interactions where one individual showed only aggressive and the other one only submissive behaviour. Aggressive behaviours used for hierarchy construction were bite, charge, chase, displace, grab, hold down, lunge, and slap, with fear scream, make room, and flee recorded as submissive behaviours (agonistic behaviours based on Kitchen et al., 2003; Ellis et al., 2011). For description of these, see Appendix II-I. Overall, 882 dyadic agonistic interactions were recorded during focal observation, with an additional 156 interactions recorded *ad libitum* (including interactions observed at the bait site), leading to an overall total of 1038 dyadic interactions usable for construction of dominance hierarchies.

Baiting and predation events

During a one-week period in June (08.06.-14.06.2017), corn kernels were widely distributed as bait around and inside a large baboon trap. The trap was located in an open field in the centre of the troop’s home-range, and the corn kernels were spread widely inside the field every day before sunrise. The baboon troop quickly adapted their behaviour and appeared at the bait site every morning. On the last day of baiting, an adult female baboon (per) was trapped and anaesthetized to be fit with a radio-collar. During this baiting period, data were collected at the bait and trap site *ad libitum* on dyadic agonistic interactions. These interactions were also used in the hierarchy calculation. In addition, focal observations were conducted once the troop left the bait site. Durations were generally shorter to make sure that as many individuals as possible were observed on each baiting day (overall 120 observations, aiming for 10-15 minutes of observation). Only individuals that were seen at the bait site (time of appearance at the bait site was noted in the morning) were observed later in the day (n = 32), to investigate whether presence at this potentially high stress site led to changes in behaviour afterwards.

After a leopard had killed a member of the troop (i.e. once in July, once in November), shorter observations, also aiming for 10-15 minutes/individual, on as many individuals as possible were also conducted during the rest of the day (both kills happened in the mornings) as well as on the following day to look for short-term changes in behaviour. As these were naturally occurring stressors, these observations were included in the general dataset in contrast to the observations conducted during the baiting period.

2.2.2.2 Data analysis

Behavioural rates

As described above, behavioural data were collected using continuous focal observations (Altmann, 1974). From these focal observations, rates of scratching, total self-directed behaviour, giving and receiving grooming, as well as aggression and agonism were calculated and corrected for observation time. Scratching, self-directed behaviour, aggression, and agonism were calculated as counts/focal hour, whereas giving and receiving grooming were measured in hours of grooming/focal hour, as this was used for calculations of the Composite Sociality Index (CSI) as well. Self-directed behaviour included scratching, yawning, and auto-grooming. Aggression included bite, grab and hold-down, charge and chase, lunge, displace, stare, and ground slap. Here, all recorded aggressive behaviours were counted towards the rate of aggression. Agonism included all aggressive behaviours, as well as submissive behaviours such as make room, flee, and fear scream. For the agonism rate, though, in contrast to the aggression rate, every agonistic interaction was only counted once towards the rate, independent of the number of different behaviours shown during the agonistic interaction. Regarding scratching, self-directed behaviours, and agonism, a new bout was counted after every 5 second break in behaviour. Table 2.3 shows mean rates of these behaviours calculated for the sexes combined and for males and females separately. These overall behavioural rates were used in investigations into long-term coping behaviours and behaviourally mediated resilience in chapters 4 and 5. Additionally, in chapter 4, changes in behaviour in response to potentially stressful situations were calculated, and these are described in detail there.

Table 2.3 Mean rates of behaviour recorded during focal animal observations, with scratching, self-directed behaviours (SDB), aggression, and agonism calculated as counts/focal hour, and giving and receiving grooming calculated as hours of grooming/focal hour. Rates are given for both sexes combined and separately for males and females.

Behavioural rate	**Overall**	**Females**	**Males**
scratching/hour	24.18	23.75	24.98
SDB/hour	27.54	26.18	30.03
giving grooming/hour	0.062	0.087	0.015
receiving grooming/hour	0.089	0.10	0.062
aggression/hour	3.01	1.9	5.03
agonism/hour	5.50	5.1	6.25

Dominance hierarchy position

As described above, agonistic behaviours recorded during continuous focal animal and *ad libitum* sampling were used to calculate dominance hierarchies. For this purpose, all dyadic interactions of clear aggression and submission, including both contact and non-contact agonistic interactions, were used. Dominance hierarchy calculations were performed using the Elo-rating procedure, which ranks individuals based on the chronological progression of recorded behaviours, in contrast to matrix-based hierarchy calculations (Neumann et al., 2011).

At the start of calculations, all individuals are assigned the same predefined rating (e.g. here 1000). During an agonistic interaction, the winner gains points and the loser loses points, with the amount of points won and lost depending on the probability of the higher-rated individual winning the interaction (i.e. based on their previous ranks) (Neumann et al., 2011). With each interaction, the ratings are updated accordingly (Neumann et al., 2011):

Higher-rated individual wins: $\text{WinnerRating}_{\text{New}} = \text{WinnerRating}_{\text{Old}} + (1 - p) \times k$

$\text{LoserRating}_{\text{New}} = \text{LoserRating}_{\text{Old}} - (1 - p) \times k$

Lower-rated individual wins: $\text{WinnerRating}_{\text{New}} = \text{WinnerRating}_{\text{Old}} + p \times k$

$\text{LoserRating}_{\text{New}} = \text{LoserRating}_{\text{Old}} - p \times k$

With p = being the probability that the higher-rated individual wins, which is a logistic function of the absolute difference in the current Elo-ratings of the two interaction partners before the start of the new interaction

k = a predefined constant that determines the amount of points lost or gained (here k = 100, following Neumann et al., 2011)

In more detail, the probability p is based on a logistic curve function of the difference in current ratings of the interaction partners. As Figure 2.5 shows as an example, if two individuals (A = square, B = circle) start with the same rating of 1000, the probability of either of them winning is p = 0.5 and therefore, if A wins, its score increases by 50 and B’s score decreases by 50. If A wins again, its score increases by 36 (as the probability of A winning is now p = 0.64). Figure 2.5 shows a sequence of 4 interactions, where A wins three interactions and B the fourth, and how the ratings change with every interaction. Note that the increase/decrease becomes smaller the larger the difference between the two individuals' ratings is, as k is multiplied with (1-p) if the higher-rated individual wins (from Neumann et al., 2011).

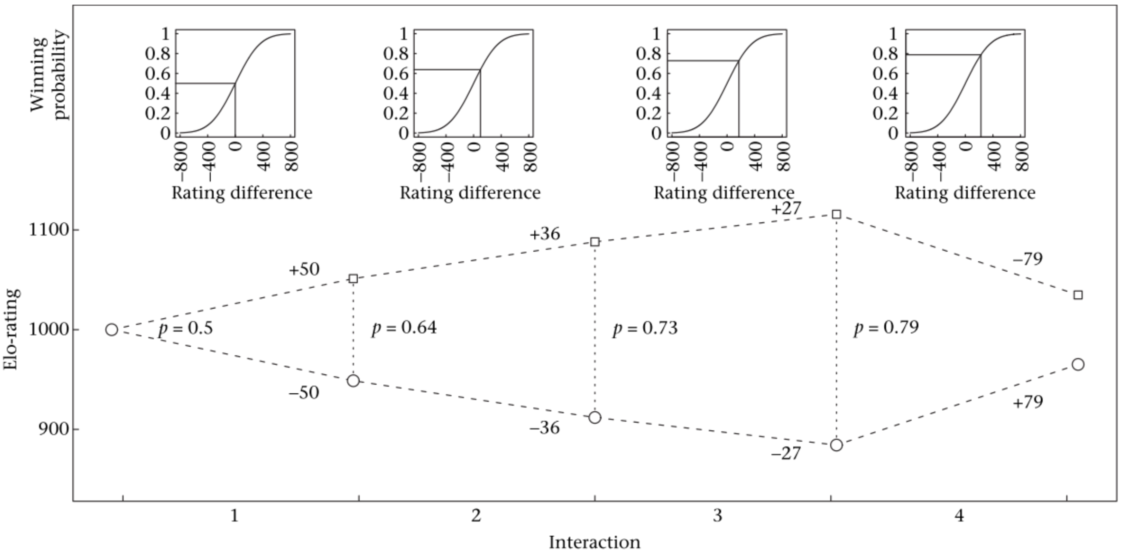


Figure 2.5 Graphic illustration of the change in Elo-ratings of two individuals based on four interactions, where A (squares) wins the first three interactions and B (circles) wins the fourth. The upper half shows the winning probability for each interaction as a logistic curve function of the difference in ratings of the two individuals before the interaction. The lower half shows the change in Elo-ratings (dotted lines) from one interaction to another, with the difference in Elo-rating before the interaction (vertical dotted line) translating to the noted probabilities based on the graphs in the upper half.
Reprinted from Animal Behaviour, vol. 82 (4), Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., Irwan, A. M., Agil, M., Widdig, A., Engelhardt, A., Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo-rating, p. 911-921, Copyright (2011), with permission from Elsevier.

Based on these calculations, the Elo-rating procedure thus enables a dynamic calculation of rank positions (Neumann et al., 2011) in contrast to matrix-based procedures such as the David Score. As several individuals disappeared throughout the study period, randomised Elo-ratings were calculated in the context of this study using the package *aniDom* (Sánchez-Tójar et al., 2018). Here, the sequence of agonistic interactions is randomised 1000 times with new Elo-ratings being calculated for each randomised sequence, and *mean* Elo-ratings are then calculated as the average Elo-rating in the 1000 randomised interaction sequences. This creates a more robust hierarchy, which can be used to try to mitigate the effect of some individuals having less interactions than others, for example due to predation or emigration. Male and female hierarchies were calculated separately, as chacma baboon males are generally assumed to be higher ranking than females. Here, there were only few exceptions, with two young adolescent males and one very old male appearing to be lower ranked than the highest-ranking females. Furthermore, almost all analyses were conducted separately for the sexes, so rank effects were generally assessed within one sex.

The development of Elo-ratings over time was visualised using the *EloRating* package in R (Neumann et al., 2011) and is shown for males in Figure 2.6. Here, the grey vertical lines mark the date of two males emigrating (fla and gor). Female Elo-ratings are shown in Figure 2.7, where the grey vertical lines mark the disappearances of three females (leopard attack on per, and disappearance for unknown reasons of sho and ste at the same time). For both males and females, disappearances of troop members do not seem to lead to drastic changes in the hierarchy. In both graphs, the effect of the baiting period in early June is striking, as it led to increased levels of observed aggression (*ad libitum* data collection at the baiting site) and clearer rank division afterwards. The baiting period is marked by a red arrow in the graphs. Elo-ratings before baiting do not necessarily seem to match the ratings afterwards, which is probably due to low levels of recorded aggression beforehand. Thus, these changes in rank do not seem to be meaningful rank reversals but to be due to methodological issues.

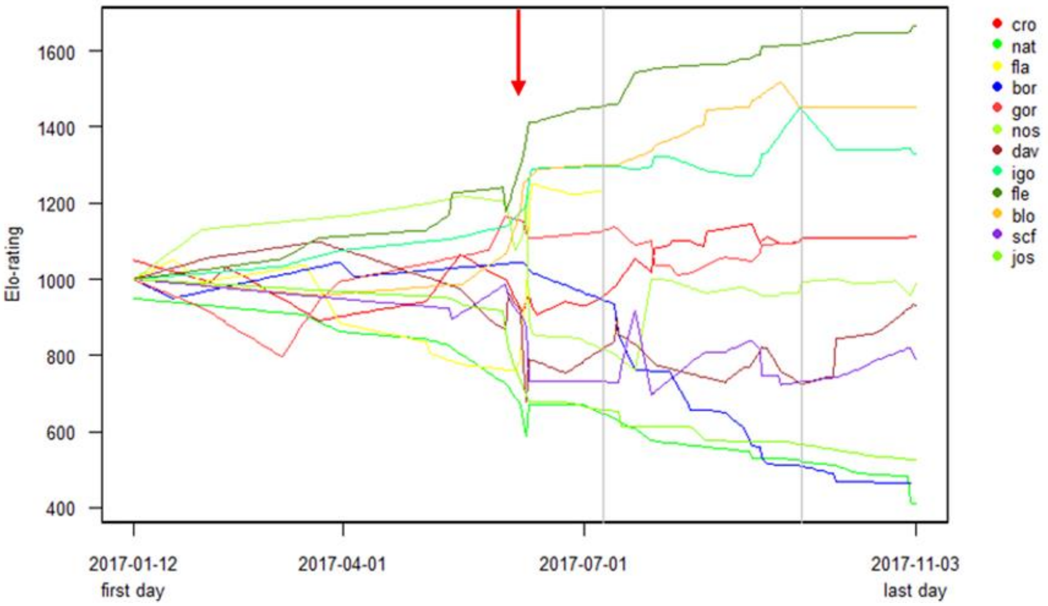


Figure 2.6 Elo-ratings of all males throughout the study period (n = 12). Grey vertical lines mark the emigration of males (fla in July, gor in September). Baiting was done in early June which led to increased observed levels of aggression at the baiting site (indicated by red arrow).

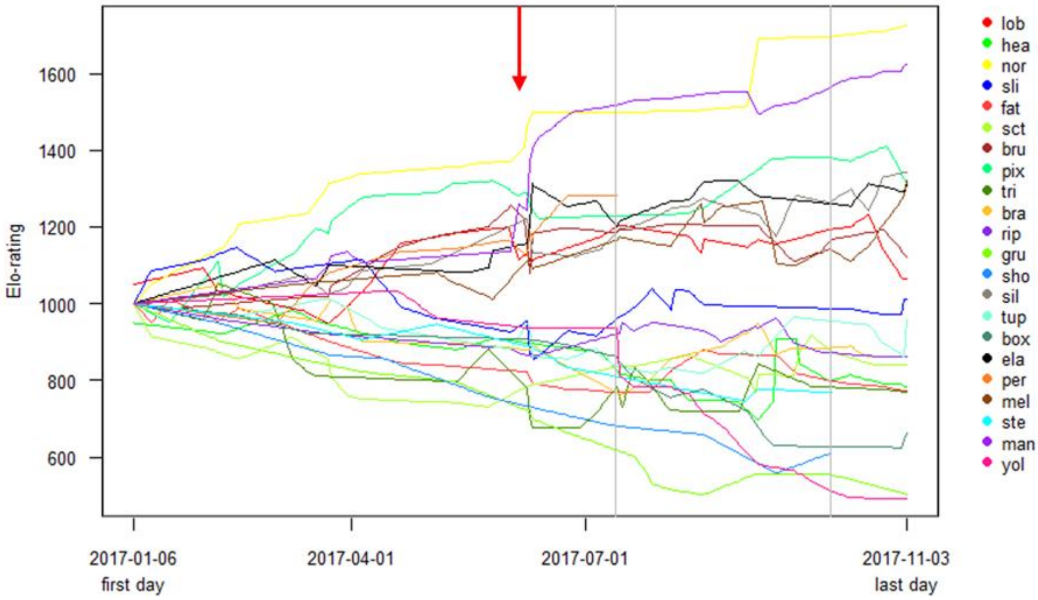


Figure 2.7 Elo-ratings of all females throughout the study period (n = 22). Grey vertical lines mark the disappearances of females (per in July, sho and ste in September). Baiting was done in early June which led to increased observed levels of aggression at the baiting site (indicated by red arrow).

To assess reliability of this method of dynamic rank calculations, firstly, randomised Elo-ratings were compared to more conservative, matrix-based normalised David Scores which were calculated using the *EloRating* package (Neumann et al., 2011) in R. Randomised Elo-ratings and normalised David Scores were highly correlated both for males and females (Pearson's product-moment correlation, males: t(10) = 19.14, r = 0.99, p < .0001, 95%-Confidence interval (CI) = 0.95, 0.99; females: t(20) = 23.45, r = 0.98, p < .0001, CI = 0.96, 0.99; Figure 2.8).

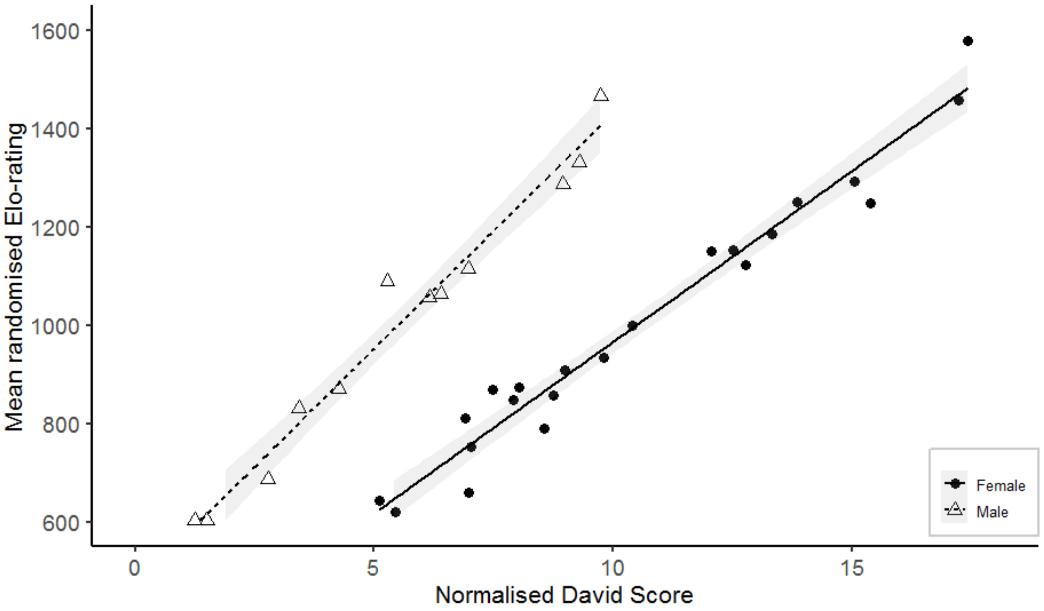


Figure 2.8 Relation of mean randomised Elo-ratings and normalised David Scores of males (n = 12) and females (n = 22). Shapes and lines mark sex, as shown in the legend. Lines represent simple linear regressions between normalised David Scores and mean randomised Elo-ratings of each sex, with shaded areas marking 95%-CIs. Both ranking scores are highly correlated with each other (Pearson's product-moment correlation, males: t(10) = 19.14, r = 0.99, p < .0001, CI = 0.95, 0.99; females: t(20) = 23.45, r = 0.98, p < .0001, CI = 0.96, 0.99).

Secondly, reliability of Elo-ratings was assessed via the randomisation procedures described above using the *aniDom* package (Sánchez-Tójar et al., 2018). Two measures of repeatability were calculated using this package: repeatability between randomisations and repeatability between the first and second half of the study period, calculated for each randomisation. Hierarchies with scores above 0.8 and above 0.5, respectively, are considered robust (Sánchez-Tójar et al., 2018). Repeatability was generally high: for males, repeatability between randomisations was 0.97 and between first and second half 0.93 (CI = 0.85, 0.98); for females, repeatability between randomisations was 0.98 and between first and second half 0.88 (CI = 0.81, 0.95). Mean randomised Elo-ratings plus 95%-CIs were thus calculated for each individual and are shown in Figure 2.9 for males and Figure 2.10 for females, with plots produced in the *aniDom* package (Sánchez-Tójar et al., 2018).

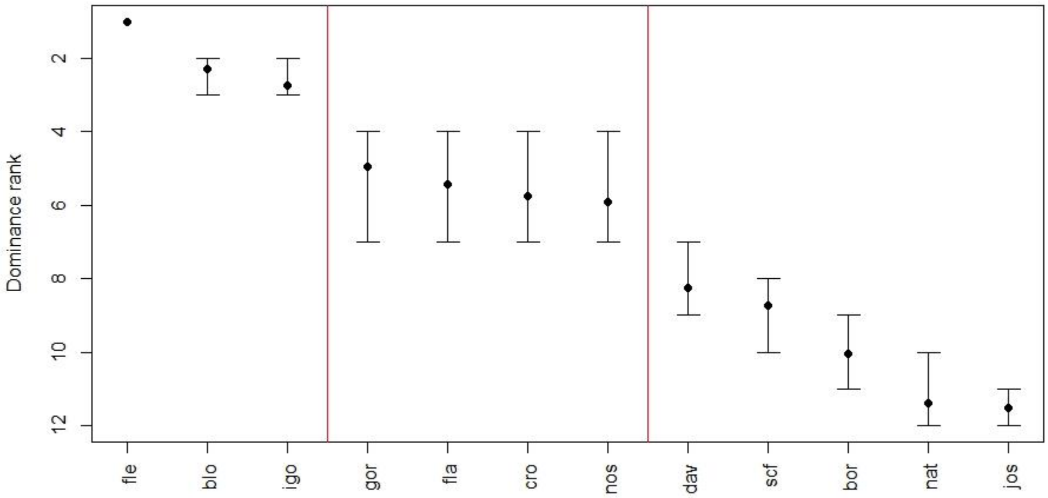


Figure 2.9 Mean randomised Elo-ratings and 95%-CIs of males (n = 12) based on 1000 randomisations of the agonistic interactions sequence. Rank categories are indicated by red vertical lines, based on peaks in the difference between mean randomised Elo-ratings (Figure 2.11) and ranks with the least overlap in CI. Plot produced in *aniDom* (Sánchez-Tójar et al., 2018).

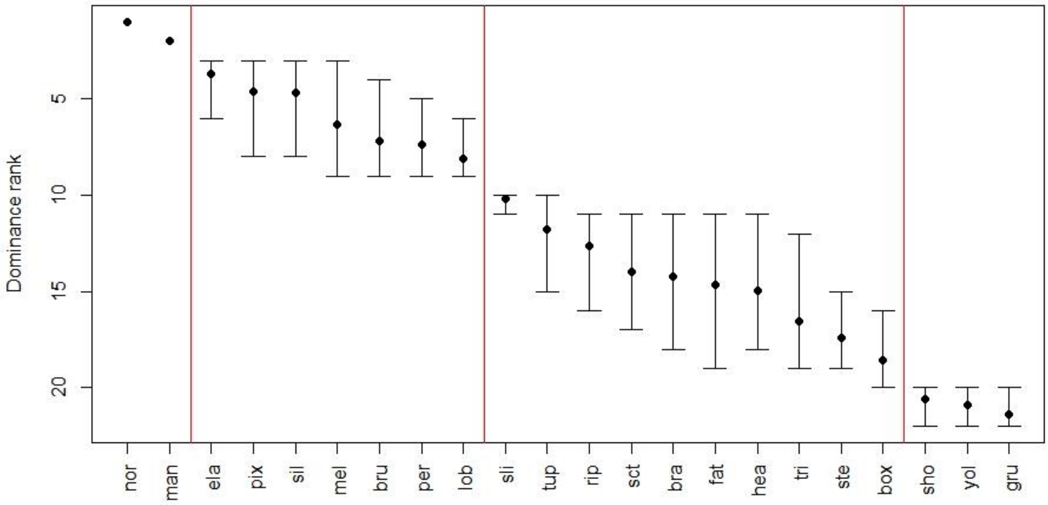


Figure 2.10 Mean randomised Elo-ratings and 95%-CI of females (n = 22) based on 1000 randomisations of the agonistic interactions sequence. Rank categories are indicated by red vertical lines, based on peaks in the difference between mean randomised Elo-ratings (Figure 2.12) and ranks with the least overlap in CI. Plot produced in *aniDom* (Sánchez-Tójar et al., 2018).

The magnitude and overlap of the CIs suggest that small differences in Elo-ratings might not be as meaningful as generally assumed but could for example be due to the probabilistic nature of observational methods, where observers will only record a small number of agonistic interactions. Therefore, the difference between neighbouring mean randomised Elo-ratings (Δ Elo-rating) was plotted against the mean randomised Elo-ratings for males in Figure 2.11 and females in Figure 2.12. Based on both assessing the peaks in these differences between neighbouring ratings and where the CI are not overlapping between ranks, rank categories were defined to group individuals of very similar ranks and overlapping CIs together. This way, males were divided into three rank categories as indicated in Figure 2.9 and Figure 2.11, while females were grouped into four rank categories as shown in Figure 2.10 and Figure 2.12.

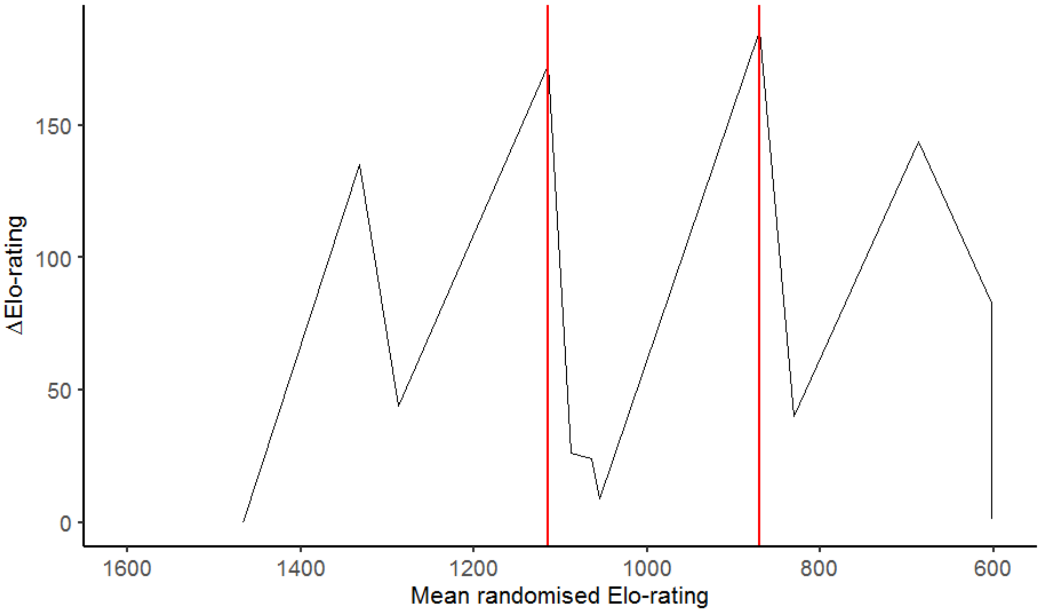


Figure 2.11 Differences between mean randomised Elo-ratings of neighbouring ranks (Δ Elo-rating) plotted against the mean randomised Elo-ratings of males (n = 12). Marked by red vertical lines are the largest differences between neighbouring ranks which are used to group ratings into rank categories.

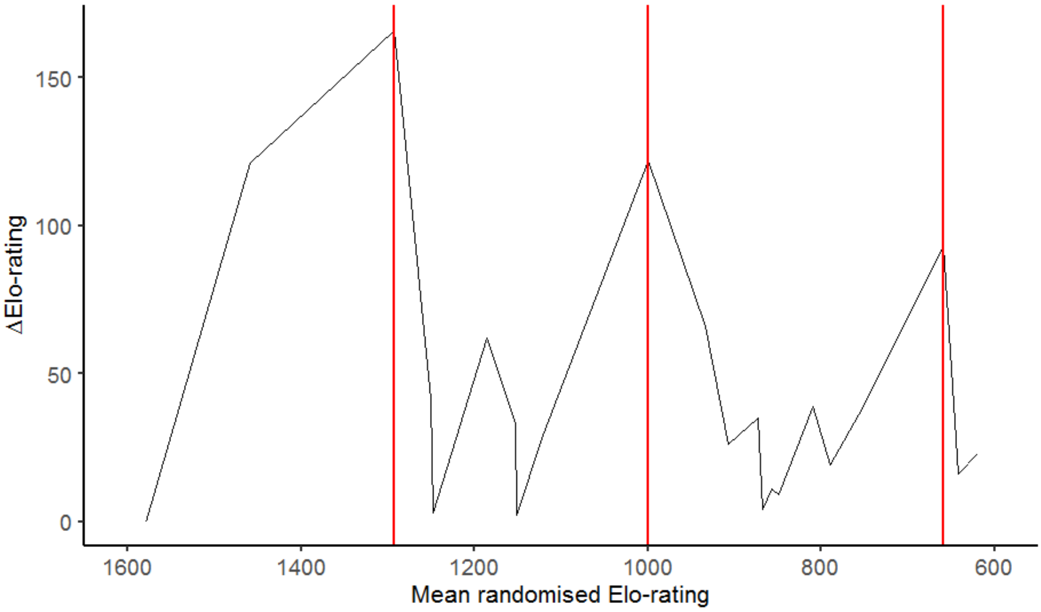


Figure 2.12 Differences between mean randomised Elo-ratings of neighbouring ranks (Δ Elo-rating) plotted against the mean randomised Elo-ratings of females (n = 22). Marked by red vertical lines are the largest differences between neighbouring ranks which are used to group ratings into rank categories.

When analysing the effect of rank on physiological stress response measures (chapter 3) and resilience (chapter 5), both the mean randomised Elo-ratings and rank category were used as predictor variables. Most studies use continuous rank position measures, such as mean randomised Elo-ratings or normalised David Scores, but the data presented in this study suggest that, at least in this population, small differences in these ratings might be due to the inherent incompleteness of behavioural observations and not necessarily reflect meaningful differences in rank. Therefore, mean randomised Elo-ratings and rank categories were compared regarding their explanatory power of physiological stress response measures and resilience. When including rank as a fixed effect in the linear models elsewhere, rank categories (as numeric values) were used to account for larger differences between these groupings, as rank categories were found to be a better predictor of mean fGCM concentrations in chapter 3.

Dyadic bond strength

Strong and consistent social bonds between individuals have been shown to play an important role in the fitness of the individuals. Probably the most widely used index to calculate affiliative dyadic bond strength is the Composite Sociality Index (CSI, Silk et al., 2006a; Silk et al., 2006b), which combines socio-positive behaviours that are highly correlated with each other. As described in chapter 1, strong social bonds, especially between females, have been connected to enhanced reproductive fitness (e.g. in yellow baboons [*Papio cynocephalus*; Silk et al., 2003]; chacma baboons [*Papio ursinus*; Silk et al., 2009, 2010b]). In chacma baboons, these bonds are always formed between mother and daughter and, to a lesser degree, between other matrilineal relatives, but are also correlated with rank and age (which might be because females of similar age and rank are potentially patrilineal siblings) (Seyfarth et al., 2014). In a study of yellow baboons, it was found that if a female lost her mother, the bonds to her maternal sisters were strengthened, whereas the bonds to maternal aunts weakened; in the absence of maternal kin, bonds to paternal kin got stronger; in the absence of any relatives, the female would invest more into bonds with non-relatives (Silk et al., 2006b). It has also been shown that the quality of the bond, i.e. the level of reciprocity of grooming calculated as the grooming equality index, influences its stability over the years, with more equitable grooming relationships being more stable (yellow baboons, Silk et al., 2006a).

While there are many different ways of assessing social bond strength, the CSI has been previously linked to various fitness-relevant measures, as described, and is as such a useful measure in the context of this study, additionally allowing for comparability with other studies. Furthermore, one could also use specific behaviours that are part of the CSI, such as grooming or body contact, as proxy for social bonds, but, as mentioned and further described below, these behaviours are highly correlated; incorporating them into one index is therefore a useful step to avoid over-testing and to avoid treating these affiliative behaviours as if they reflect different aspects of social bonds, which they likely do not.

While most of these studies have investigated female-female bonds, recent studies have shown that baboons maintain opposite-sex bonds over longer time periods (chacma baboons, Baniel et al., 2016; olive baboons [*Papio anubis*; Städele et al., 2019]) and that the presence of these also predicts longevity in female baboons (yellow baboons, Archie et al., 2014). Therefore, dyadic CSI values were calculated for all pairs of the study subject, including both same- and opposite-sex bonds, as both of these might play important roles in the context of stress buffering and resilience.

The dyadic CSI was calculated for each pair of baboons based on frequency and duration of close proximity (i.e. < 1.5m, Prox), frequency and duration of body contact (Bc), and frequency and duration of grooming interactions (Gr) (following Haunhorst et al., 2017; Müller-Klein et al., 2019). The frequencies and durations were found to be significantly correlated with each other, with the lowest correlation coefficient being r = 0.41 between the duration of proximity and the duration of grooming. Durations and frequencies were then divided by the group means and CSIs were calculated using the following formula (Silk et al., 2013):

$$CSI = \frac{\left(\frac{F_{Prox}}{mean(F_{Prox})} + \frac{D_{Prox}}{mean(D_{Prox})} + \frac{F_{Bc}}{mean(F_{Bc})} + \frac{D_{Bc}}{mean(D_{Bc})} + \frac{F_{Gr}}{mean(F_{Gr})} + \frac{D_{Gr}}{mean(D_{Gr})}\right)}{6}$$

where F = frequency (count/focal hour)

D = duration (behaviour in hour/focal hour) of the respective behaviour

For body contact and grooming, only interactions that were at least 5 seconds long were included, and a new interaction was counted following a break of at least 5 seconds. Durations and frequencies were corrected for the observation time during which both interaction partners were potentially available, i.e. if an individual disappeared during the study period, only the observation times up until that point in time of both interaction partners were used for the specific dyad.

As has been described before (Silk et al., 2006b), the distribution of CSI scores was strongly skewed to the left (Figure 2.13). By the way the CSI is calculated, the group mean is always 1, but the group median was 0.24 (0.27 for females and 0.21 for males), reflecting the high number of weak bonds individuals of both sexes had. Only about 19% of dyads had a CSI above one, thus reflecting, by the definition used here, a relatively strong bond. On average, females had 7.82 strong bonds (min - max: 5 - 12) and 23.82 weak bonds (min - max: 20 - 28), while males had on average 3.67 strong bonds (min - max: 0 - 7) and 27 weak bonds (min - max: 20 - 31). Regarding the top three bonded partners of each individual, whose scores were used to calculate the sum of the top three CSIs, males had generally females as their top three partners, with only one exception where the third strongest bond was to another male, but the CSI was below one. Two males had generally low bond strength, i.e. all their CSI scores were below one; one of these was an adolescent male rising in rank, the other was a very old male. For females, the sex of their top three bonded partners was more variable: less than half (i.e. 10 out of 22 females) had only other females as their top three bonded partners, while 9 females had one male as a top three partner, and for three females, two out of the top three bonded individuals were males.

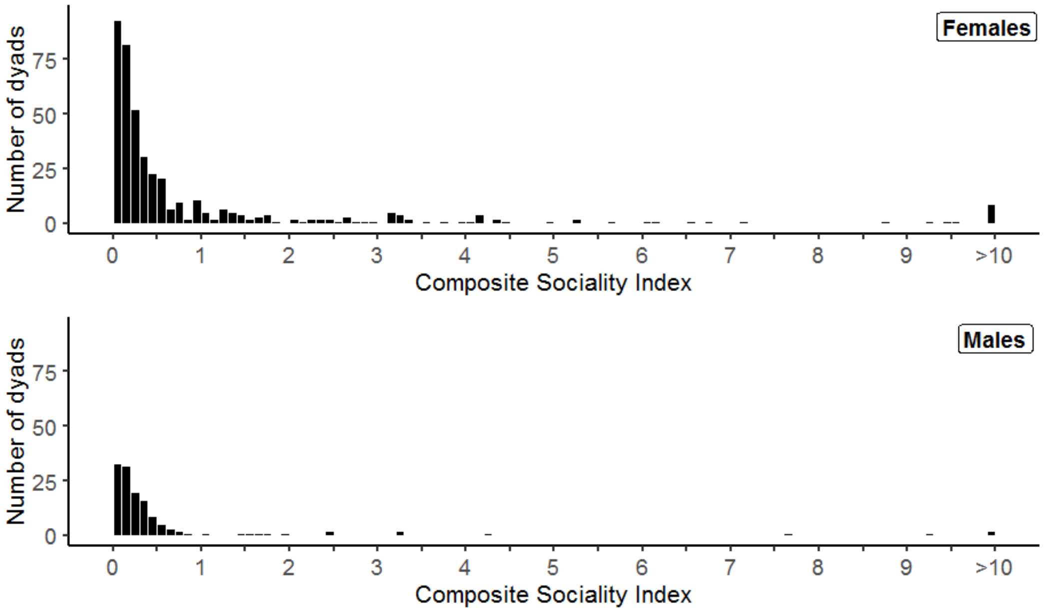


Figure 2.13 Distribution of Composite Sociality Index (CSI) values, with female values depicted in the top graph, and male values depicted in the bottom graph. CSI values are plotted on the x-axis, and number of dyads are plotted on the y-axis. Each bar indicates the number of dyads that had a CSI value of the magnitude indicated on the x-axis (n = 561 dyads).

For all analyses using bond strength, the sum of their top three CSI values was calculated for each individual, as well as their number of relatively 'weak' bonds with

CSIs < 1, and their number of relatively ‘strong’ bonds with CSIs > 1, in line with McFarland et al. (2017). By definition, the group mean of CSIs is one, so these represent the number of stronger and weaker than average bonds an individual had. While this creates an artificial dichotomy, i.e. there are no medium strength bonds, using these measures allows us to add another level of explanation regarding the link between sociability and fitness, where not only the strength of the bonds but also the number of bonds an individual has might play an important role. Moreover, the commonly and also here used ‘sum of top three CSI values’ includes an arbitrarily chosen number of partners, where some individuals might have many more strong bonds that are not included, while others have no bonds with CSIs above one, so that all of their ‘strong bonds’ are bonds of below average strength compared to the other group members. Thus, including different ways of using CSI scores might enable us to assess different aspects of sociability; there are more ways one could use CSI scores, e.g. one might use the sum of all above average strength bonds, but the here used measurements have been linked to fitness-relevant measures before (e.g. Silk et al., 2010b; McFarland et al., 2017) and were thus used for comparability reasons. Generally, the sum of the top three CSI values is thought to reflect the strength of an individual’s strongest bonds, i.e. whether an individual has very strong bonds compared to its troop members, while a high number of strong bonds might indicate that an individual focusses not solely on a few strongly bonded partners but maintains above average relationships to a larger number of individuals and is generally very sociable. A large number of weakly bonded partners was here thought to indicate that an individual was generally well integrated, in the sense that they have low-frequency affiliative interactions with, or at least are in the proximity of, a large number of individuals.

Even though non-social bonds with a CSI of zero were excluded from the number of weak bonds (McFarland et al., 2017), the number of strong and the number of weak bonds were highly negatively correlated (Pearson's product-moment correlation, t(28) = -14.86, r = -0.94, p < .0001, CI = -1, -0.89), due to the number of non-social bonds being very low. Furthermore, the sum of the top three CSI scores was positively correlated with the number of strong bonds an individual maintained (Pearson's product-moment correlation, t(28) = 3.13, r = 0.51, p = .004, CI = 0.18, 0.73), i.e. individuals that had many above average strength bonds were more likely also to have very strong bonds, even though the correlation coefficient was only r = 0.51 and the 95%-CI was relatively large. In line with this, the sum of the top three CSI scores was negatively, but relatively weakly, correlated with the number of weak bonds (Pearson's product-moment correlation, t(28) = -2.35, r = -0.41, p = .026, CI = -0.67, -0.05), indicating that individuals who have many below average strength bonds also tend to have relatively weak strongest bonds. Here, visual depiction (Figure 2.14) suggests that this might be especially true for males, as males with a larger number of weak CSI values tended to have lower sums of their top three CSI values. Exploratory analysis fittingly showed that for males a large number of weak bonds was linked to weaker top three bonds (Pearson's product-moment correlation, t(9) = -3.18, r = -0.73, p = .011, CI = -0.92, -0.23), while these two measures were not correlated in females (Pearson's product-moment correlation, t(17) = 0.29, r = 0.07, p = .779, CI = -0.4, 0.51).

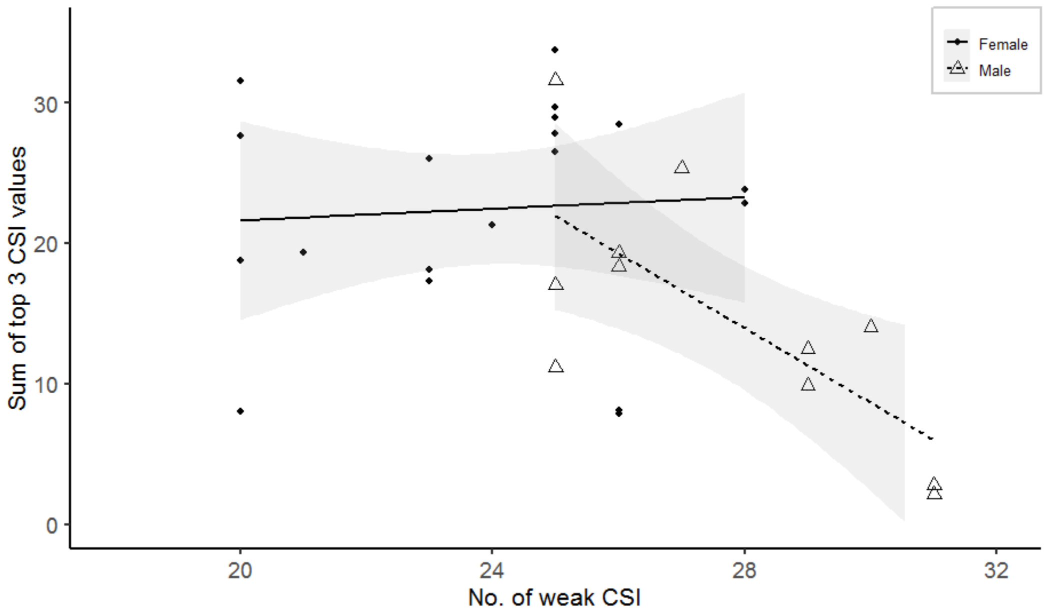


Figure 2.14 Males' and females' sum of their top three Composite Sociality Index (CSI) values in relation to their number of weak CSI values, with weak CSIs being defined here as being below the group average of one. Shape and line type indicate sex as noted in the legend. Lines represent simple linear regressions between the sum of top three CSI values and the number of weak bonds, with shaded areas marking 95%-CIs (Pearson's product-moment correlation, both sexes: t(28) = -2.35, r = -0.41, p = .026, CI = -0.67, -0.05; males: t(9) = -3.18, r = -0.73, p = .011, CI = 0.92, -0.23; females: t(17) = 0.29, r = 0.07, p = .779, CI = -0.4, 0.51).

In addition to these measurements, the strength of the strongest bond, i.e. the highest CSI value an individual had, was used in the analyses to account for the possibility that individuals might only have one very strong bond, which might play an important role in the context of social buffering, for example, but that, in comparison to individuals with many above average strength bonds, they would have lower sums of their top three CSI scores. In line with above described correlations, the value of the highest CSI was strongly positively correlated with the sum of the top three CSI scores (Pearson's product-moment correlation, t(28) = 10.72, r = 0.9, p < .0001, CI = 0.79, 0.95), suggesting that individuals who have one very strong bond tend to have several strong bonds.

As these different measures of bond strength and sociability were highly correlated with each other, separate models were calculated including either the number of strong or the number of weak bonds, the sum of the top three CSI scores, or the highest CSI value. These measures of the strength of an individual’s strongest bonds, as well as the number of its weak and its strong bonds were investigated in relation to physiological stress response measures in chapter 4 and to resilience measures in chapter 5.

Social network position

As briefly mentioned in chapter 1 and described in more detail in chapter 4, social integration and the size of an individual’s network, assessed for example via social network analysis, have been linked to fGCM levels (chacma baboons [*Papio ursinus*; Crockford et al., 2008; Wittig et al., 2008]; rhesus macaques [*Macaca mulatta*; Brent et al., 2011]) and other fitness-relevant measures, such as infant survival (chacma baboons, Cheney et al., 2016) and survival during extreme weather conditions (Barbary macaques [*Macaca sylvanus*; McFarland and Majolo, 2013; Lehmann et al., 2015]). Therefore, social network analysis was performed for one affiliative and one agonistic network. The affiliative network was based on the dyadic CSI values described above (following Cheney et al., 2016), while the agonism network was based on the hourly rate of all aggressive and submissive interactions recorded during focal observations (following Lehmann et al., 2015), thus using the same data that was used for calculation of agonistic interaction rates mentioned above but excluding interactions with unidentified interaction partners. As the main interest was in the effect of general social integration, and to be able to compare the predictive value of social integration measured either via affiliation or agonism, both networks were constructed as undirected networks. Additionally, using symmetric networks makes some network metrics more readily interpretable, e.g. eigenvector centrality, and ensures that the same data are used for all network metrics as some metrics, such as individual clustering coefficient, are only defined for undirected networks (Lehmann et al., 2015). Networks were constructed including all study subjects, but subsequent analyses using the calculated network metrics were done separately for males and females. Some individuals had to be excluded from these as physiological stress response or resilience measures were not available.

For both networks, some commonly used metrics of general social integration were calculated (Brent et al., 2011; Lehmann et al., 2015; Cheney et al., 2016): for both the affiliation and agonism network, weighted strength, eigenvector centrality, betweenness centrality, and individual clustering coefficient as well as unweighted reach were calculated, with binary degree added for the agonism network. Table 2.4 gives an overview of the metrics calculated for each network and details on which edges were used for calculation. Unweighted (or binary) *degree* indicates the number of interaction-partners an individual had over the study period. Degree was therefore calculated for the agonism network, reflecting the number of individuals with which the subject animal had at least one agonistic interaction, but was not calculated for the affiliation network, as this would be similar to the number of strong and weak bonds described above. *Strength* (also called weighted degree) reflects the tie strength between the subject and all its interaction partners, i.e. the frequency with which the interactions take place. Individuals with a high degree have therefore many interaction partners, while individuals with high strength have interactions at a high rate. While degree and strength are calculated solely based on direct connections, the remaining metrics include both direct and indirect connections in the network.

Eigenvector centrality reflects the quantity and quality of an individual's partners as well as the quantity and quality of the partners' partners. Thus, an individual with high weighted eigenvector centrality has many partners, with which it interacts frequently, who themselves also have many partners, with which they interact frequently. *Betweenness centrality* is often used to assess the importance of an individual for network cohesion, as it measures how often the individual represents the shortest path between two other individuals, taking into account the number and strength of ties equally. Thus, high betweenness centrality indicates that an individual plays an important role in connecting otherwise unconnected dyads and is therefore considered central to the network. *Individual clustering coefficient* is a measure of cliquishness, i.e. how well-connected one’s partners are amongst themselves, with the weighted clustering coefficient taking into account the strength of ties, i.e. the frequency of interactions. High individual clustering coefficients indicate strong local clustering, whereas low clustering coefficients indicate that connections are evenly spread and, thus, that there are no strong subgroupings. For the affiliation network, only edges larger than the mean CSI of one were included, thus only considering relatively strong bonds, as the network was generally very dense, i.e. there were only few dyads with a CSI of zero as described above. Unweighted *reach*, finally, describes the number of individuals the subject can reach in *k* (here 2) or fewer steps, i.e. it sums up the number of direct connections an individual has and the number of indirect connections within two steps. Thus, reach provides another measure of the size of an individual’s local network, i.e. individuals with high reach have many partners who themselves have many partners. As was done for the clustering coefficient, for the calculation of reach only edges larger than the mean CSI of one were included in the affiliation network, and only edges that were at least as strong as the mean were included in the agonism network, due to the high density of the networks. Selection of network metrics generally followed Tkaczynski (2017), Cheney et al. (2016), Lehmann et al. (2015), and Brent et al. (2011).

Additionally, network density was calculated for both the affiliation and the agonism network as a comparative measure of overall network connectivity. Density is calculated as the ratio of observed edges to all possible edges in the network (Wasserman and Faust, 1994). Both networks constructed here were comparatively dense. When including all CSIs, the network density was 0.95 (i.e. 95% of all possible connections between dyads had a CSI above zero), which is unsurprising as the CSI calculation included proximity in addition to body contact and grooming. When including only CSI values above the average of one (i.e. ‘strong’ bonds as defined in this study; these edges being used for the calculation of individual clustering coefficient and reach), density was lower at 0.20. Density of the agonism network was 0.61 when including all edges and 0.42 when only including edges ≥ mean, these being the edges that were used for the calculation of reach in the agonism network.

Table 2.4 Overview of the network metrics calculated for the affiliation and the agonism network, including whether weighted metrics were calculated, which edges were included, and a short description of the metrics (Brent et al., 2011; Lehmann et al., 2015; Cheney et al., 2016).

	Affiliation NW		**Agonism NW**		
Metric	**Weighted?**	**Edges**	**Weighted?**	**Edges**	**Description**
Degree	-	-	Unweighted	All	The number of interaction-partners an individual has.
Strength	Weighted	All	Weighted	All	Reflects the frequency with which interactions between an individual and all its partners take place.
Eigenvector centrality	Weighted	All	Weighted	All	Reflects the quantity and quality of partners an individual has, as well as the quantity and quality of partners they themselves have.
Betweenness centrality	Weighted	All	Weighted	All	Represents the number of shortest paths between otherwise unconnected dyads that go through the individual.
Individual clustering coefficient	Weighted	CSI > 1	Weighted	All	A measure of cliquishness, i.e. how well-connected one’s partners are among themselves.
Reach (*k* = 2)	Unweighted	CSI > 1	Unweighted	≥ mean	The number of individuals the subject can reach in two or fewer steps.

All network metrics were calculated in R (R Core Team, 2018). Strength and reach were calculated with simple R functions, while degree, eigenvector centrality, and individual clustering coefficient were calculated using the *igraph* package (Csardi and Nepusz, 2006), and betweenness centrality was calculated using the *tnet* package (Opsahl, 2009). Networks were visualised using NetDraw in Ucinet (Borgatti et al., 2002), with nodes, i.e. circles or squares, representing individuals and edge width, i.e. width of the lines connecting nodes, reflecting the strength of the relationship between the two individuals. Codes and details on the calculations are compiled in Appendix II-II.

The link between individual network metrics and the respective response variables was assessed via model comparisons, as described in the respective chapters. Models that received substantial support in the model comparison then underwent a node permutation test with 1000 randomisations (Farine and Whitehead, 2015). Here, the edges were kept constant, while the identity of the nodes was randomised and for each randomisation the model was newly calculated. Subsequently, the estimate of the original model was compared to the 1000 estimates acquired by the randomisation procedure, and the p-value was calculated based on how many estimates were smaller or larger than the original estimate. Only significant results ($p < .05$) acquired through this procedure were discussed further. The network metrics of the affiliative and agonistic networks were used in investigations regarding the links between network position and physiological stress response measures (chapter 4) and measures of resilience (chapter 5).

2.2.3 Faecal glucocorticoid metabolite concentration measurement

2.2.3.1 Sample collection and analysis

Faecal sample collection

Faecal samples were collected from all subjects opportunistically by ZM, AS, and AA, resulting in 363 faecal samples collected overall. Samples were collected as quickly as possible, at the latest 15 minutes after defecation. Samples were only collected if the individual was seen defecating and clearly identified, and the samples were not contaminated by urine or other faeces. Samples were homogenised using a gloved hand, and a small portion (thumbnail size, 2-5 g) stored in a pre-numbered container labelled with subject ID, date, time, and collector. Samples were stored on ice in a cooler bag during a field day and stored in a freezer at -20°C as soon as possible thereafter, at the latest at the end of the day.

Faecal sample collection was made challenging by the difficult terrain and individual differences in level of habituation and general behaviour; thus, the number of samples for each individual varied greatly. As physiological stress response measures were calculated based on monthly averages, only those individuals for which samples from at least four different months were available were included. Thus, four individuals had to be excluded from the analyses (three old females, one adolescent male), as they either disappeared before enough samples could be collected, or because sample collection was difficult for them. Overall, 30 subjects were included, with a range of monthly averages available of 4 to 10 monthly samples/individual (mean ± SD = 6 ± 1) (similar range to Ellis et al., 2011). If two or more samples were collected on the same day, only the first sample/day was used. As there can be a diurnal pattern in faecal hormone metabolite excretion (Moreira et al., 2016), the effect of time of day on fGCM concentrations was tested, as will be described further below.

Samples were kept frozen until transport on ice in cooler boxes to the University of Pretoria, Faculty of Veterinary Medicine, at the end of the study period. Here they were freeze dried and subsequently shipped to the University of Roehampton, UK (see Appendix I-II for import license and conditions).

Grinding and hormone extraction

All faecal samples were analysed at the Hormone Laboratory of the University of Roehampton, UK. Firstly, all dried samples were ground into fine powder using pestle and mortar and then passed through a fine meshed sieve to remove undigested material such as seeds and grass. Between 0.080 - 0.097 g/sample of faecal powder were used for further analysis.

Steroid hormone metabolites were extracted from the weighed faecal powder using 3 ml Methanol (>95%). Solutions were shaken for 10 minutes and subsequently placed in a centrifuge at 4500 rpm for 20 minutes at 4°C. The supernatant was removed and stored at -20°C. The efficiency of the extraction procedure was determined by monitoring the recovery of radio-labelled steroid (^{3}H oestradiol), which was added to a separate subsample of 8 faecal samples before extraction, and which found that 72.04% - 84.48% of radio-labelled steroid were recovered (mean 78.91%) (Möhle et al., 2005).

Enzyme immunoassay

Hormone analysis was conducted using enzyme immunoassay (EIA) (Lequin, 2005). Analysis was done using a competitive binding assay, 5β-androstane-3α,1β-diol-17-one, which has been validated in other baboon species (Higham et al., 2009). EIA procedures followed those described by Heistermann et al. (2004), with more detail presented in Appendix II-III.

Both standard solutions and faecal extracts were diluted in assay buffer (0.04M phosphate-buffered saline, pH 7.2). A reference standard curve was created using serial dilutions of the standard solution resulting in 9 different dilutions, ranging in concentration from 1.22 to 312.5pg/50µl. To estimate the best dilution factor for analysis of the study samples, 6 samples were chosen with assumed low, medium, or high hormone levels (based on reproductive and social status) and each diluted at five different concentrations ranging from 1:40 to 1:640. These dilutions were assessed for parallelism in relation to the standard curve: Figure 2.15 depicts the measured optical densities of the six samples in relation to the standard curve and shows that the measured fGCM behave similarly to the standard curve made of known concentrations. Using the results of this test, a dilution of 1:100 was selected for analysis of samples, as this would most likely result in samples falling into the linear range of the standard curve. Only concentrations of four samples did not fall into the linear range of the standard curve, two of which were subsequently diluted at 1:200 and two of which were diluted at 1:25 for analysis.

Microtiter plates with 96 wells were used for EIA, which were previously coated with anti-rabbit immunoglobulin G, developed in sheep. Ascent software (Thermo Labsystems, 2002) was then used to calculate EIA concentrations; from this, fGCM levels could be then calculated correcting for dry faecal weight, dilution factor, and extraction efficiency:

$$fGCM = \frac{EIA\ concentration\ (pg/50\mu\text{l})\ x\ Extract\ volume\ (3000\ \mu\text{l})\ \text{x Dilution factor x}\ (100/factor\ 78.91)}{Dry\ faecal\ weight\ (g)\ x\ Sample\ volume\ (50\mu\text{l}) x\ 1000\ *}$$

** units conversion factor (pg to ng; 1000)*

(Dilution factor was generally 100; 200 for two samples, and 25 for two samples

as described above.)

Sensitivity of the assays at 90% binding was 2.0pg/50µl. Mean intra-assay coefficients of variation, calculated from repeated measures of high and low concentration quality controls, were 5.1% for high (n = 11 plates) and 5.8% for low (n = 12 plates). Inter-assay coefficients of variation were 10.5% (high, n = 23 quality controls) and 13.0% (low, n = 24 quality controls).

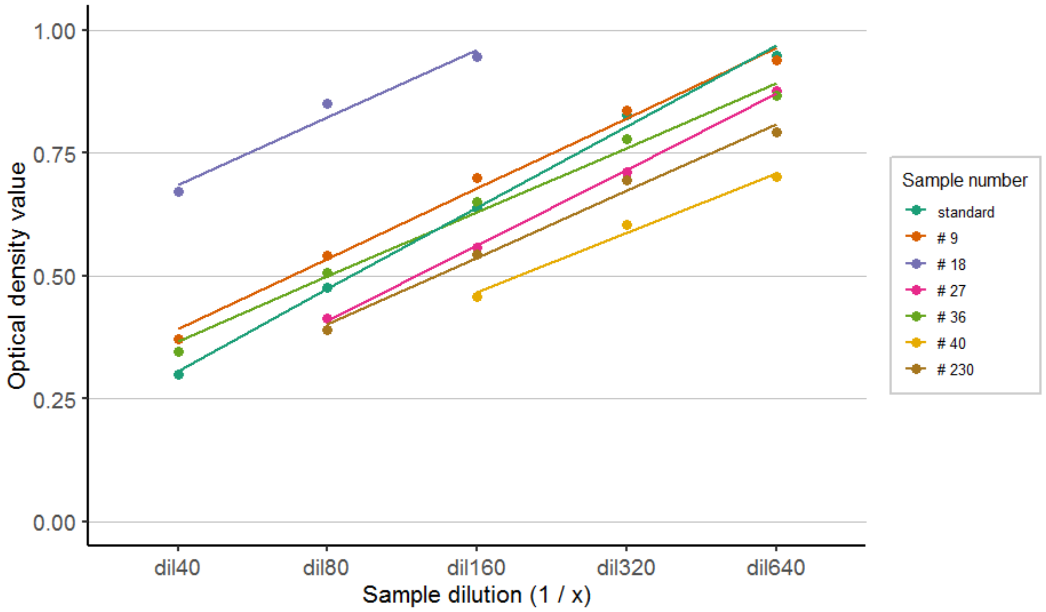


Figure 2.15 Parallelism test for 6 samples plotting regression lines of optical density values against sample dilutions (ranging from 1:40 to 1:640) in relation to the standard curve. Colour reflects sample number or standard curve as indicated by the legend.

2.2.3.2 Treatment and preliminary analysis of fGCM data

Demonstrated reactive scope and mean fGCM concentrations

As described in chapter 1, this study uses demonstrated reactive scope (MacLarnon et al., 2015) as a non-invasive proxy for stress reactivity. The demonstrated reactive scope is based on the reactive scope model (Romero et al., 2009), which has been described in detail in the previous chapter, and is as such assumed here to reflect the range of mediator an individual uses over a specific time period to deal with the experienced challenges, reflecting stress reactivity during this time period. To reiterate, DRS was calculated as a percentage based on monthly mean fGCM concentrations for individuals for which faecal samples of at least four months were available (males n = 11, females n = 19), using the following formula:

$$DRS_X = ((X_{max} - X_{min}) / X_{min}) \times 100$$

Additionally, a coefficient of variation (DRS_{CV}) was calculated with n as the number of months for which samples were available, based on the same monthly mean fGCM concentrations:

$$DRScv_X = (\text{standard deviation}_X / \text{mean}_X) \times (1 + 4 / n)$$

To allow a comparative analysis of stress reactivity, as represented by demonstrated reactive scope, and long-term levels of physiological stress response mediators, the latter was calculated as mean fGCM concentrations based on the same monthly mean fGCM concentrations used for the calculation of demonstrated reactive scope. As such, three physiological stress response measures were available for every individual, i.e. the mean fGCM concentration, DRS, and DRS_{CV}. Table 2.5 gives an overview of the group means of these three measures, as well as the means and ranges of the measures for each sex.

Table 2.5 Overview of means and ranges of physiological stress response measures, showing both group means and means for each sex as well as ranges of each sex for mean fGCM concentrations as well as demonstrated reactive scope, measured as DRS and DRS_{CV}.

	Mean fGCM	**DRS**	**DRS_{CV}**
group mean	1965.22	313.62	0.77
males mean:	1899.9	178.17	0.58
min - max:	1353.98 - 2391.93	40.13 - 414.39	0.22 - 1.23
females mean:	2003.04	392.03	0.88
min - max:	1402.06 - 2649.9	45.92 - 2254.51	0.36 - 2.36

Factors influencing fGCM concentrations

There are several factors that might influence measured hormone metabolite concentrations. Some of these, such as sex, age, reproductive state, and dominance rank position, were investigated in initial analyses in chapter 3, as were effects of different weather variables and adverse events, such as predation. When investigating the effect of environmental factors on GC concentrations, an excretion lag between circulating hormone levels and hormone metabolites measured in faeces needs to be considered. Marked steroid hormone metabolites have been shown to be measurable in faecal samples after 24-72 hours, with peaks measured after 26-36 hours (Wasser et al., 1994; Wasser et al., 2000), so in line with common practice I used a time lag until excretion of 2 days (Higham et al., 2009). Additionally, fGCM concentrations might follow a diurnal pattern. In black capuchin monkeys (*Sapajus nigritus*), for example, higher levels of excreted GC derivates have been found in the morning than during the rest of the day (Moreira et al., 2016), whereas in Bornean orangutans (*Pongo pygmaeus*) and mountain gorillas (*Gorilla beringei beringei*), for example, no such patterns were found (Amrein et al., 2014; Eckardt et al., 2016). Here, the effect of time of day was tested using a paired t-test, comparing fGCM concentrations of morning samples with fGCM concentrations of afternoon samples of individuals for which two samples were collected on the same day. There was no statistical difference between morning and afternoon samples (paired t-test, t(6) = 0.73, p = .496, CI = -174.51, 321.48; n = 7), so time of day was not included as a factor in models.

Hierarchy instability is also known to influence fGCM levels in male chacma (*Papio ursinus*) and olive baboons (*Papio anubis*) (Bergman et al., 2005; Sapolsky, 2005), as well as in female chacma baboons depending on their reproductive state (i.e. in lactating and pregnant females, Beehner et al., 2005). Inspection of visual representation of Elo-rating development over the study period in Figure 2.6 and Figure 2.7, however, does not reveal any clear phases of rank stability or instability, and permutation procedures

– as described in section 2.2.2.2 – revealed stable and robust hierarchies across the study period. Thus, no phases of rank stability could be defined and therefore rank stability was not further investigated in its potential link to fGCM concentrations.

2.2.4 Measures of coat condition

Coat condition was assessed using two different methods, with one being more conventional visual coat condition ratings conducted by two observers, and the other being the development of a new measure of coat insulation quality using infrared thermography. These measures of coat condition were used in chapter 5 for the assessment of resilience and will be described in detail there.

Coat condition ratings

As studies in captive rhesus macaques (*Macaca mulatta*) showed no significant difference between coat condition ratings by eye and ratings derived from photographs (Honess et al., 2005), coat condition was assessed via visual ratings during observations by two independent observers. Following the method of Maréchal (2015), the ratings were made once a month (from June to November - 6 ratings/individual), thus assessing the development of coat condition over the course of the dry season, which is the season of increasing food scarcity, while avoiding effects that high humidity and rainfall can have on the appearance of the fur (Maréchal, 2015). Each individual was rated on a scale from 1 (bad coat condition) to 10 (perfect coat condition). Considered in these ratings were the coverage of fur (i.e. whether any fur was missing), the quality of fur (shiny vs wiry), and the coat on the tail (the coat on the tail was often patchy in the subject animals). Only the coat on head, back, sides, legs, and tail were considered, as the coat quality in the stomach area might not be related to the condition on the other body parts (Borg et al., 2014; Maréchal, 2015). Ratings were avoided on rainy days and only done on misty days if these conditions persisted, as high humidity can change the appearance of the coat (Maréchal, 2015). However, as all individuals were rated at the same time (i.e. on the same day, or exceptionally the following day), the effects of variation in humidity were assumed to be similar for every individual, thus not influencing inter-individual differences. Coat condition ratings of 6 timepoints were available for 29 individuals (males n = 10, females n = 19), while for one male and two females only 4 ratings were available, as they emigrated or disappeared before the end of the study. Testing for inter-observer reliability, there was significant agreement between the two observers (one-way Single Score Intraclass Correlation (ICC): ICC = 0.64, n = 189, raters = 2, F(188,189) = 4.51, $p < .0001$, CI = 0.54, 0.72; conducted using the *irr* package, Gamer et al., 2019). Ratings of the two observers were averaged for each month. Based on these ratings, two measures of coat condition were calculated: first, an average coat condition based on the averaged monthly ratings was calculated, and second, the relative change in coat condition over the dry season calculated in percent as:

$$\text{Relative change} = ((\text{end condition} - \text{start condition})/\text{start condition}) * 100$$

While the measure of relative change does not incorporate the ratings in between the first and last month, coat condition does not change drastically from month to month and small differences between individual months are more likely to be linked to the subjectivity of scoring. Using only the first and last month, however, gives a general idea of whether individuals increased or decreased in their coat condition over the dry season. Additionally, ratings of all months are incorporated for the calculation of average coat condition, so this measure takes into account whether, for example, an individual received high ratings over longer time periods and decreased only at the end, or whether it decreased right at the beginning and then stayed constant at a lower score (which would not necessarily be reflected by the relative change measure). That is likely also the reason why average coat condition and the relative change in coat condition were not correlated in males (Spearman's rank correlation, S = 175.17, rho = 0.20, p = .548, n = 11) or females (Spearman's rank correlation, S = 1600.8, rho = -0.20, p = .389, n = 20), indicating that they might reflect different aspects of physiology or general well-being.

Infrared thermography

Infrared pictures were taken of the 27 individuals that were well enough habituated (n = 11 males, n = 16 females) using a FLIR E8 thermal camera (model FLIR-E63900, IR resolution 320x240 pixel, thermal sensitivity < 0.06°C, accuracy ± 2% of reading), and temperatures were determined using FLIR tools software (version 5.7.16168.1001). Pictures were taken of the side of an animal's trunk, where a continuous coat covers the body, while they were standing or walking; for each individual between 1 and 4 pictures were available (mean ± SD = 2.07 ± 1.07), with the low sample size and the low number of pictures per individual being due to many baboons being not well enough habituated to such data collection, the frequent movement of the baboons, and the difficult terrain that was not conducive to such measurements. Temperature measurements were taken from a rectangle, located between the animal's shoulder and hip crease, as shown in Figure 2.16. Care was taken not to measure the temperature too far upwards towards the back, to avoid problems with increased reflection due to the curve of the body, and to keep distance from the lesser covered skin of the belly, thus avoiding the more thinly covered area of the abdomen. It is not easily possible to standardise the size and placement of this rectangle to the body shape and size of the individual or the angle at which the picture was taken, so as a future refinement to the method it would be helpful to investigate further the effect of different body sizes and of inter-individual differences in how body parts are covered by coat on these temperature measurements, and to explore further if and how a standardisation is possible. In the context of this study, though, experimental small changes in placement and size of the rectangle did not lead to any substantial changes in measured temperatures. Thus, from inside this rectangle, the minimum and maximum temperatures were determined as well as the average temperature in the rectangle using FLIR tools. From the maximal and minimal temperature, a delta coat temperature was calculated, which I propose provides an index of the homogeneity or uniformity of the coat, and thus its insulation quality. Additionally, the maximal skin temperature on the abdomen (outside of the pictured rectangle) was determined as a proxy for actual skin temperature. For all subsequent analyses three temperature measurements are used:

- delta coat temperature in °C (maximum - minimum temperature from within the rectangle)
- average coat temperature in °C (calculated in FLIR tools within the rectangle)
- abdominal maximum skin temperature in °C (the maximum skin temperature on the animal’s trunk, measured outside of the rectangle)

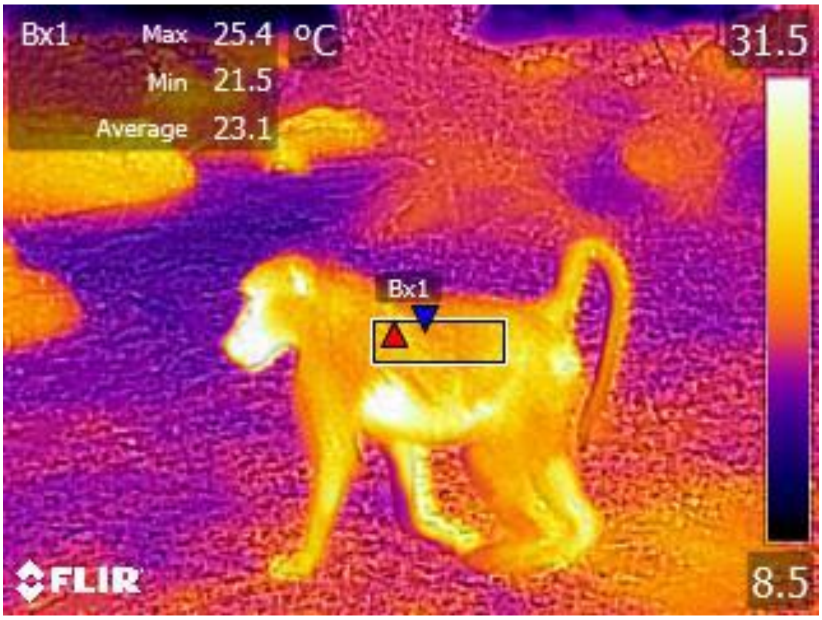


Figure 2.16 Example of a thermal picture of an adult male baboon. The rectangle shows the analysed area for measuring the average coat temperature (23.1°C) as well as the minimum (21.5°C) and maximum (25.4°C) temperatures used to calculate delta coat temperature. Maximal abdominal skin temperature was measured outside of this rectangle but is not shown here (picture taken with FLIR E8 thermal camera, analysed with FLIR Tools).

For the FLIR tools software to accurately determine temperatures, several environmental factors need to be entered into the software for each picture, i.e. ambient temperature, relative humidity, distance between animal and camera, emissivity, and reflected temperature. Ambient temperature and relative humidity were taken from the data collected by the weather station described in this chapter, and the distance of the subject to the camera was estimated from the size of the animal in the picture. While the latter is not a precise measure of distance, small differences in this setting (approximately ± 2m distance) do not appear to lead to changes in the measured temperatures, as only significantly larger differences in distances (e.g. if a picture was taken at more than 10m distance, or if the setting was set to 1m instead of 3m distance) would lead to such changes, so this approximation works well-enough for the purpose here; all pictures were taken from distances between 1.5m and 6m. Furthermore, emissivity of the coat was set in the software for all pictures to 0.86, as McGowan et al. (2018) found this to be the mean emissivity of the fur of different animal species. While they also found that emissivity varied between individuals and body parts, this is probably still a better estimate than the previously suggested and used 0.98 of human skin (Thompson et al., 2017b). Ideally, reflected temperature should be measured within each picture taken, by including a crumpled and re-flattened piece of aluminium foil to measure the radiation coming off other objects and being reflected from the object in question. However, this was not practically possible with such fast-moving and easily startled animals, so reflected temperature was set to 20°C for all measurements. While this might affect the actual temperatures measured, delta coat temperature was only slightly, if at all, altered by experimentally setting the reflected temperature in the software to different values. As solar radiation will affect temperature readings of fur due to reflection, pictures were only taken if the animals were in the shade, before sunrise or after sunset.

When several pictures were available for an individual, raw values of the three measurements were used to test for inter-individual differences (using ANCOVAs), to investigate the effect of environmental factors on these three measurements, and to explore the association between the measurements, with the models for the latter two including individual ID as random factor. When looking at potential sex differences, mean values of average coat temperature, delta coat temperature, and maximum abdominal skin temperature were used, with mean delta coat temperatures also used for the subsequent calculation of resilience.

2.2.5 Additional data collected

Reproduction and survival

Data on reproduction and survival were collected during the field work period and supplemented by data from previous years (data available from 2014 onwards) and data from a period after the end of data collection (i.e. November 2017 to October 2018), all provided by the Primate and Predator Project. Details on survival during the study period can be found in Table 2.1 and Table 2.2.

While reproduction for females is relatively easy to quantify (the exception is miscarriages), this is a lot more difficult for males if no DNA paternity data are available. There are three main reasons for this: (i) not all matings might actually be observed, for example if matings are surreptitious; (ii) some males might invest more mating effort in highly fertile females, or in conceptive versus non-conceptive cycles of females; (iii) sperm competition or sperm selection might play a role and thus mating effort might not directly relate to mating success (Alberts et al., 2006). Thus, while females' reproductive state and their reproductive success in the last three years were investigated regarding their links to fGCM concentrations and resilience (chapter 3 and 5, respectively), males' reproductive success could not be reliably assessed in the context of this study and was therefore not further investigated in how it might link to physiological stress response measures or resilience.

Injuries and illnesses

In addition to reproduction and survival, *ad libitum* data were also collected on injuries individuals sustained and whether they showed sickness behaviour, which suggests illnesses or infections. Open wounds sustained during fights with conspecifics or predators provide an entryway for bacteria and parasites. Thus, they are a major health concern as the risk of infection and immobility increases, which can also lead to severe complications and an increased risk of predation and mortality (Archie, 2013; Maréchal, 2015). While the probability of sustaining injuries might not necessarily be linked to resilience, sustaining severe injuries or infections due to superficial injuries could affect subsequent resilience to other stressors or further infectious agents. However, occurrence of wounds and infections was so low that it was not appropriate to do statistical testing.

2.2.6 Overview of methods used

For a general overview of the types of data collected, the calculations done with each type of data, and the use of the data in the different analyses and chapters, see Table 2.6. Faecal samples were collected to assess fGCM concentrations, as these are thought to reflect the energetic demands an individual experiences, e.g. linked to environmental variation, life-history stage, or aversive situations that elicit a stress response. Thus, fGCM levels were analysed regarding their link to environmental factors and reproductive state, while long-term physiological stress response measures (i.e. mean fGCM concentrations, DRS, and DRS_{CV}) were analysed regarding variation between different life-history stages and regarding inter-individual differences in these measures linked to coping behaviours or sociability. Demonstrated reactive scope was also used in the calculation of resilience.

Coat condition was assessed via coat condition ratings and via IRT, as a useful non-invasive ‘measure of success’ in dealing with everyday life. Thus, different measures of coat condition were explored regarding their link to environmental factors, it was tested whether different measures of coat condition were correlated with each other, and three measures of coat condition were subsequently used in the calculation of resilience.

Data on reproductive state of females were collected to investigate the link between reproduction and fGCM concentrations. Additionally, reproductive success over several years (i.e. the number of surviving offspring a female had, whether a female lost an infant in the last three years, and whether she was lactating during the study period) was explored regarding its link to resilience, as it was hypothesised either that more resilient females might have higher reproductive success, or that high reproductive output or the loss of an infant might take a toll on the female and could lead to lower resilience over time.

While the use of fGCM concentrations, coat condition measures, and reproductive factors is relatively straightforward, the use of behavioural data collected throughout this study is more varied. Firstly, regarding *ad libitum* sampling, dyadic agonistic interactions were recorded, which were only used for the calculation of dominance rank position, and matings and consortships were noted, which were only used to assess the time point at which females became pregnant.

Secondly, using continuous focal animal sampling, three main types of behaviour were recorded, i.e. affiliative (or socio-positive) behaviours like giving and receiving grooming, self-directed behaviours such as scratching, and agonistic behaviours such as aggressive and submissive behaviour. These were previously proposed to potentially be coping behaviours in non-human primate species, so it was investigated whether they increased after aversive events (baiting and predation), and whether high long-term rates of these behaviours were linked to lower physiological stress response measures (i.e. mean fGCM levels, DRS, or DRS_{CV}), all of which would be interpreted as reflecting the ‘successful’ use of coping behaviours. In line with this, these long-term behavioural rates were also investigated regarding their link to resilience, where it was hypothesised that, if resilience was behaviourally mediated, higher rates of coping behaviours would be connected to higher resilience.

Finally, using data on proximity, body contact, and grooming collected during focal animal observations, dyadic CSIs were calculated as a measure of social bond strength. Using CSIs, it was investigated whether different measures of sociability, e.g. the strength of an individual's strongest bonds or the number of its strong and weak bonds, were linked to lower physiological stress response measures, potentially reflecting social buffering, or were linked to higher resilience, in line with the social buffering hypothesis. Additionally, it was explored whether social integration measured via social network position, in contrast to sociability assessed via dyadic bond strength, was linked to lower physiological stress response measures or higher resilience, potentially shining a light on the importance of indirect connections in addition to direct connections between individuals. As it has been shown before that social integration assessed via agonistic social networks might better explain inter-individual variation in fitness and survival than integration assessed via affiliative social networks, here both an affiliative social network, based on the dyadic CSIs, and an agonistic network, based on rates of aggressive and submissive behaviours recorded during focal animal sampling, were used to determine social network position.

Table 2.6 Overview of the different types of data collected throughout the study, the use of the data (i.e. the types of measures calculated using the recorded data), and details on where each type of data and calculated measures were used (i.e. chapter and analysis).

Type of data collected	Use of data/calculated measures	Used in analyses
Behavioural data Continuous focal animal sampling: - Affiliative behaviour - Agonistic behaviour - Self-directed behaviour	Continuous focal animal sampling: - overall rates of behaviour (grooming given and received, aggression given, general rate of agonism, scratching, all self-directed behaviours) - change in behaviour after predation and baiting - dyadic bond strength (via Composite Sociality Index) - social integration in affiliation or agonism network (via social network analysis)	Chapter 3: - dominance rank position (link to mean fGCM, DRS, DRS_{CV}) Chapter 4: - change in behaviour rates (link to change in fGCM or mean fGCM, DRS, DRS_{CV}) - overall rates of behaviour - bond strength - social integration (link to mean fGCM, DRS, DRS_{CV})

Ad libitum sampling: - Dyadic agonistic interactions	*Ad libitum* and continuous focal animal sampling: - Dominance rank position (Elo-ratings, normalised David Score)	Chapter 5: - dominance rank position - overall rates of behaviour - bond strength - social integration (link to resilience)
fGCM concentrations	Sample fGCM concentrations Long-term measures: - mean fGCM concentrations - DRS - DRS$_{CV}$	Chapter 3: - Sample fGCM concentrations (link to climate variation and reproductive state, change of fGCM levels in response to predation) - Long-term measures (link to demographic factors: inter-individual differences, sex, age, dominance rank position) Chapter 4: - Changes in sample fGCM concentrations (link to changes in behaviour after predation or baiting) - Long-term measures (link to changes in behaviour after predation or baiting, link to overall behavioural rates, link to social bond strength or social integration) Chapter 5: - DRS and DRS$_{CV}$ used for the calculation of resilience - mean fGCM levels (link to resilience)
Coat condition	Coat condition ratings: - average coat condition - relative change in coat condition IRT: - delta coat temperature - average coat temperature - abdominal maximum skin temperature	Chapter 5: - exploration of IRT measurements - average coat condition, change in coat condition, delta coat temperature used for calculation of resilience
Reproduction	Reproductive state Reproductive success: - number of surviving infants - loss of infant in last three years	Chapter 3: - reproductive state (link to sample fGCM concentrations) Chapter 5: - reproductive state (link to coat condition, link to resilience) - reproductive success (link to resilience)

2.3 Statistical analysis and modelling approaches

For all data, normality was assessed using the Shapiro-Wilks test (Field et al., 2012) in combination with visualisation of distribution patterns. Generally, parametric tests were preferred and, if needed, data were transformed to normality using $\log_2$- or $\log_{10}$-transformations. Subsequently, hypotheses were tested using ANOVAs or ANCOVAs, paired or independent t-tests, and Pearson's product-moment correlations, depending on the question. In the case of ANOVAs, post-hoc testing was done with Tukey multiple comparisons of means where appropriate. Where transformation to normality was not possible, Wilcoxon signed-rank tests of paired data and Mann-Whitney U tests of independent data were used. All tests were conducted two-tailed and p-values with an $\alpha < .05$ were considered significant. Details on tests and transformations used can be found with the respective results.

When testing several predictors simultaneously, general linear models (LM) or general linear mixed models (LMM) were constructed, as detailed with the respective results. Following Crawley (2007) and Bolker et al. (2009), only variables with at least five levels should be included as random factors, so while individual ID had an appropriate amount of levels, age or rank classes for example did not and were therefore included as fixed effects; these were then also kept in the null models as fixed effects. LMMs were constructed using the *lme4* package (Bates et al., 2015), and the *lmerTest* package (Kuznetsova et al., 2017) was used to obtain p-values of fixed effects. Additionally, 95%-CI were calculated using the generic R *stats* package, and marginal and conditional R^2 effect sizes (Nakagawa and Schielzeth, 2013) in percent were calculated using the *MuMIn* package (Barton, 2019).

For all models, it was tested whether all model assumptions were met. Specifically, normality of residuals was assessed using Q-Q plots, homoscedasticity of residuals was assessed by plotting residuals against fitted values, and multicollinearity was tested for using Variance Inflation Factors in the *car* package (Fox and Weisberg, 2019). Conservatively, VIFs < 2 (as discussed in Zuur et al., 2010) and correlations between fixed effects below r = 0.6 (following Gesquiere et al., 2008) were accepted and fixed effects excluded if multicollinearity occurred. Additionally, Cook's distances were calculated to determine influential data points using the *influence.ME* package (Nieuwenhuis et al., 2012); if a data point had a Cook's distance > 1, the model was run again without this data point and results of models were compared. It is important to note that influential data points are not necessarily outliers, and that points that look like outliers are not always influential data points, as data points are 'influential' if they have an unusually large effect on the results of regression analysis; thus, Cook's distance determines the effect of deleting data points on the regression results (Field et al., 2012).

Regarding LMs, testing of assumptions was additionally done using the *gvlma* package (Pena and Slate, 2019). If model assumptions were not met, response variables were transformed to normality using $\log_2$- or $\log_{10}$-transformations, normality was assessed via the Shapiro-Wilks-test (Field et al., 2012) and histogram visualisation, and assumptions were reassessed. If transformation was not possible, potentially violated model assumptions are noted with the results.

Model selection was based on an information-theoretic approach (Burnham and Anderson, 2002). As this is a fundamentally different approach to null hypothesis testing, significances of p-values of fixed effects are reported for information purposes only. Probability of models, however, was assessed using second-order information criterion (AIC_C, similar to AIC but corrected for small sample sizes), AIC_C differences (ΔAIC_C, $AIC_{C(i)}$-$AIC_{C(min)}$), Akaike weights (ω), and the Evidence ratio based on Akaike weights (Burnham and Anderson, 2002). Models with $\Delta AIC_C > 2$ compared to the model with lowest AIC_C were assumed to be considerably less likely to be the best model of the set given the respective data (Burnham and Anderson, 2002). Thus, only models with $\Delta AIC_C < 2$ or strikingly large effect sizes compared to the null model, indicating that the additional fixed factor of the full model explained a substantial part of the response variable's variation, were considered to have received substantial support in the model comparison (Burnham and Anderson, 2002). Regarding effect sizes, defining cut-offs of what constitutes a 'small' or 'large' effect size is difficult and depends on the biological system studied (Nakagawa and Cuthill, 2007). In social sciences, an R^2 of 0.04 has been suggested as a small effect, of 0.25 as a moderate effect, and of 0.64 as a strong effect (Ferguson, 2009). Here, as sample sizes were relatively low and interpretation was based on correlational evidence, full models with effect sizes that were at least 10% larger than the effect size of the model with the lowest AIC_C were considered potentially meaningful, even if they had a $\Delta AIC_C > 2$. Generally, these models had effect sizes above 20%, which I would regard as a moderate effect based on the guidelines described above.

All statistical analyses were conducted in R version 3.5.1 (R Core Team, 2018). All graphs were created using the *ggplot2* package (Wickham, 2016). Data are depicted where possible as scatter plots, with boxplots added for categorical factors and asterisks indicating significance levels. Here, boxes show the inter-quartile range (IQR), while vertical lines note medians, and whiskers go out to 1.5x the IQR or the furthest point within this range. Outliers are added outside of this. Data points were jittered horizontally to avoid over-plotting and to enhance visibility. For continuous variables, regression lines are only added in exceptional situations, for clearer representation of the described associations, based on simple linear models between the predictor and response variable shown in the graph and including a 95%-CI. Influential data points are marked by an asterisk in plots.

3. Physiological stress response levels and stress reactivity in chacma baboons: demographic and environmental factors

3.1 Introduction

As described in chapter 1, the activation of the HPA-axis in response to stressors is a vital part of an animal's general stress response that enables it to survive and reproduce. This chapter describes a first investigation into individual variation in demonstrated reactive scope (DRS, and coefficient of variation: DRS_{CV}) as a measure of stress reactivity and compares this measure of stress reactivity with individuals' mean physiological stress response levels, measured as mean fGCM concentrations. To do this, mean fGCM levels and demonstrated reactive scope are first compared between the sexes, and across age groups, female reproductive states, and dominance rank positions; this initial set of analyses provides a basis for further investigation into physiological stress response measures in chapter 4. Next, the effects of environmental factors, i.e. weather variables and predation events, on individuals' fGCM levels are investigated. While stress in wild baboons has been studied for nearly 30 years, few studies have investigated populations living in montane habitats, even though it has been suggested that habitat type might be of great importance in this regard due to its influence on social organization and environmental challenges (Hinde, 1983; Henzi and Barrett, 2003). Therefore, this chapter aims to provide basic knowledge of mean physiological stress response levels and reactivity of males and females of a montane chacma baboon population.

3.1.1 Demographic factors

Sex differences

Regarding differences between the sexes in GC levels, not many studies have investigated these differences, or even males and females simultaneously, in non-human primates. In rats, however, there seems to be some consensus that females have higher basal corticosterone levels than males (Nelson, 2005) and also higher concentrations in response to HPA-axis stimulation (Kudielka and Kirschbaum, 2005; Nelson, 2005). In several non-human primate species, studies found similar sex differences. Studies in long-tailed macaques (*Macaca fascicularis*) and black capuchins (*Sapajus nigritus*) found that females tended to have higher mean uGCM and fGCM concentrations than males (van Schaik et al., 1991; Moreira et al., 2016). Similarly, Eckardt et al. (2016) found that female mountain gorillas (*Gorilla beringei beringei*) had higher baseline fGCM levels than males, and Tkaczynski (2017) showed that Barbary macaque females (*Macaca sylvanus*) had higher mean fGCM concentrations than males. These findings of sex differences in hormone concentrations are not unexpected as males and females differ considerably in their physiology and reproductive systems, hormonal interactions, and organisational effects of their hormonal pathways, as well as in body sizes in sexually dimorphic species (with hormone levels generally being assumed to be lower in larger animals) (Romero and Wingfield, 2015). Males and females also differ in their social behaviour and thus in the social stressors they experience; for example, females experience higher energetic demands and various social stressors linked to reproduction and infant care, while males might experience agonistic interactions linked to dominance rank acquisition and maintenance as social stressors. Therefore, an investigation into sex differences in mean fGCM levels in this baboon population could inform the picture by broadening the range of species considered.

Regarding stress reactivity, only one study to my knowledge has investigated sex differences in demonstrated reactive scope of GCs. In Barbary macaques (*Macaca sylvanus*), males and females did not differ in their DRS_{CV} (DRS was not tested) (Tkaczynski, 2017).

Age

Generally, non-human primate species seem to experience infant hypercortisolism, with a subsequent decline of GC levels through juvenile and adolescent stages and a rise in hormone levels with the start of adulthood (e.g. olive baboons (*Papio anubis*) and hamadryas baboons (*Papio hamadryas*); Fourie et al., 2015). When only investigating adult individuals though, as a majority of studies do, most often no correlation was found between fGCM levels and age, either in females (rhesus macaques [*Macaca mulatta*; Brent et al., 2011; Qin et al., 2013]; chacma baboons [*Papio ursinus*; Beehner et al., 2005; Engh et al., 2006b]) or males (bonobos [*Pan paniscus*; Surbeck et al., 2012]; yellow baboons [*Papio cynocephalus*; Gesquiere et al., 2011b; Gesquiere et al., 2011a]; chacma baboons, Bergman et al., 2005). However, a few studies did find such associations. In yellow baboons, GC levels of both males and females seem to increase with age (Sapolsky and Altmann, 1991; Alberts et al., 2014), while in long-tailed macaques (*Macaca fascicularis*) the results are more complex: in females, GC levels decreased with age only in non-lactating females but not others, whereas hormone levels of males were lower for old low-ranking males than for other age-rank groups (van Schaik et al., 1991). These varying results suggest that the effect of age on fGCM levels might potentially be of interest in the context of this study and might link to different stressors animals experience – and how they cope with them – based on their life-history stage.

Reproductive state

While different reproductive states are linked to different, partly predictable, social and environmental stressors which can affect GC levels (Landys et al., 2006), there are also physiological changes between reproductive stages connected to GC concentrations. During a mammalian pregnancy, plasma CRH concentrations, for example, increase exponentially due to CRH being produced in the placenta, decidua (the mucosal lining of the uterus), and foetal membranes (Mastorakos and Ilias, 2003). Thus, ACTH secretion increases, and the rising levels of plasma ACTH cause a rise in plasma GC concentrations (Mastorakos and Ilias, 2003). Therefore, pregnancy can be described as a transient form of hypercortisolism (Mastorakos and Ilias, 2003), with GC levels increasing with the month of pregnancy (as found in rhesus macaques [*Macaca mulatta*; Brent et al., 2011]). In non-human primates, these increased levels of GC during pregnancy were for example found in chacma baboons (*Papio ursinus*; Weingrill et al., 2004; Beehner et al., 2005; Engh et al., 2006b), rhesus macaques (Brent et al., 2011), mandrills (*Mandrillus sphinx*; Setchell et al., 2008), white-faced capuchins (*Cebus capucinus*; Carnegie et al., 2011), and chimpanzees (*Pan troglodytes*; Murray et al., 2018).

During lactation, females of many mammalian taxa, such as rodents, tufted capuchins, and humans, undergo a phase of reduced GC reactivity (reviewed in Rodrigues et al., 2015). This effect seems to be species-specific and potentially linked to species- or habitat-specific questions of energetic costs, infant care, and perceived threat to the infant (Rodrigues et al., 2015). In Geoffroy's spider monkeys (*Ateles* *geoffroyi*), for example, females have lower GC levels during lactation than during cycling, which could potentially be explained by the very low risk of infanticide in the species (Rodrigues et al., 2015). A decrease of GC concentrations during lactation could also be linked to increased levels of oxytocin. During suckling, the somatosensory stimulation leads to a rise in oxytocin which in turn can lead to a decrease in GC concentrations and other stress-related measures (Uvnäs-Moberg, 1998). Contrastingly, high energetic or infant care demands, as well as high levels of perceived threat of infanticide, can in turn lead to an increase in GC concentrations during this reproductive state (Rodrigues et al., 2015). Such an increased level of GCs in lactating compared to cycling females was for example found in chacma baboons (*Papio ursinus*; Weingrill et al., 2004) and rhesus macaques (*Macaca mulatta*; Hoffman et al., 2010).

Overall, reproductive state seems to influence GC levels in many ways: while there are physiological effects linked to pregnancy and lactation, the perceived threat to the infant, the protection it needs, and the effort it takes to cover maternal energetic needs can also affect GC levels. Therefore, the effect of reproductive state on fGCM levels will be investigated in this study and reproductive state will be, where appropriate, included as a correction term in further analyses to cover these basic physiological differences.

Rank

The relationship between stress and dominance rank has been studied for nearly 40 years, and during this time a more and more complex picture of this link in non-human primate species has evolved. Depending on the species and sex (and potentially habitat), some studies find a link between rank and physiological stress response levels, some no link at all, and others a link that seems to be dependent on a variety of factors.

Across species, the association between rank and physiological stress response levels seems to be more consistent for males than for females.

In male yellow baboons (*Papio cynocephalus*), for example, lower ranking individuals had higher GC levels than high-ranking individuals (Sapolsky et al., 1997), with the most dominant male also having an exceptionally high fGCM concentration in this species (Gesquiere et al., 2011a). Similar negative correlations were found in olive baboons (*Papio anubis*; Sapolsky, 1982; Abbott et al., 2003), Assamese macaques (*Macaca assamensis*; Ostner et al., 2008), and Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*; Yang et al., 2016). To my knowledge, only one study on male chacma baboons has found that high-ranking males have higher fGCM concentrations than low-ranking males (Kalbitzer et al., 2015). The remaining studies found the correlation to be context dependent: high-ranking bonobo (*Pan paniscus*) males, for example, had higher uGCM concentrations than low-ranking males when in the presence of oestrus females, whereas there was no such difference if no oestrus female was present (Surbeck et al., 2012). Besides the presence of receptive females, hierarchy stability seems to be the main source of variation in this context. During stable times, low-ranking male chacma baboons tend to have higher fGCM levels than high-ranking individuals, while this correlation reverses during times of hierarchy instability (Bergman et al., 2005), with the same pattern being described in mandrills (*Mandrillus sphinx*; Setchell et al., 2010).

In contrast to males, there are more studies of female non-human primates that have not found a correlation between dominance rank and physiological stress response levels, for example in chacma baboons (*Papio ursinus*; Weingrill et al., 2004; Beehner et al., 2005; Engh et al., 2006b), mandrills (*Mandrillus sphinx*; Setchell et al., 2008), rhesus macaques (*Macaca mulatta*; Brent et al., 2011), long-tailed macaques (*Macaca fascicularis*; van Schaik et al., 1991; Stavisky et al., 2001), and white-faced capuchins (*Cebus capucinus*; Carnegie et al., 2011). In studies finding a correlation, the nature of the association depended on the species; subordinate females often had higher GC levels than high-ranking females, as was found in female chacma baboons (measured as fGCM, Seyfarth et al., 2012), yellow baboons (*Papio cynocephalus*; plasma levels, Sapolsky et al., 1997), and Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*; measured as fGCM, Yang et al., 2016), whereas in Barbary macaques (*Macaca sylvanus*) and ring-tailed lemurs (*Lemur catta*) high-ranking females had higher fGCM levels than females of low rank (Gustison et al., 2012; Cavigelli and Caruso, 2015). Studies in female rhesus macaques (*Macaca mulatta*) found again more complex relations, in that the link between physiological stress response levels and rank either seemed to be dependent on the type of hierarchy, i.e. only in less stringent hierarchies did low-ranking females have higher GC concentrations (measured in hair, Qin et al., 2013), or was found to be mediated by an interaction of rank and a social network measure of connectedness (proximity reach) (measured as fGCM, Brent et al., 2011).

Overall, it seems that the presence and direction of a link between dominance rank and physiological stress response levels often depends on the strategies or challenges connected to rank acquisition and maintenance (Abbott et al., 2003). While in many species males fight for high ranks and therefore have either generally higher GC levels when being of high rank (e.g. Kalbitzer et al., 2015) or at least during times of hierarchy instability (e.g. Setchell et al., 2010), low-ranking males potentially experience more social stress during times of stable hierarchies and have thus higher GC concentrations then (e.g. Abbott et al., 2003; Setchell et al., 2010). Contrastingly, females often inherit ranks from their mothers and have therefore low chances of increasing their rank through aggressive encounters, which could explain why physiological stress response levels often do not vary with dominance rank (e.g. Setchell et al., 2008). Thus, the species-specific mechanisms of rank acquisition and questions of rank (in)stability should be considered when investigating the link between rank and physiological stress response levels in non-human primates.

Importantly, no study has yet investigated whether demonstrated reactive scope varies with dominance rank position. Using a similar idea, though, it was found in female ring-tailed lemurs (*Lemur catta*) that high-ranking females had higher mean fGCM concentrations but similar minimum values compared to low-ranking females (Cavigelli and Caruso, 2015). Thus, the difference in means was caused by higher maximum GC concentrations and thus higher stress reactivity instead of chronically elevated GC levels, a differentiation that might have important fitness implications (Cavigelli and Caruso, 2015). This idea of combining mean stress levels with comparisons of maximum and minimum values is conceptually comparable to the model of demonstrated reactive scope.

3.1.2 Environmental factors

Weather

Extreme weather conditions can considerably influence wild animals, their behaviour, and their hormone levels, and can cause animals to enter the so-called ‘emergency life-history stage’ (Romero and Wingfield, 2015). It is not only extreme, but also daily, seasonal or annual variation in weather and daylight duration that influences animals and might pose challenges that they need to cope with, which might lead to changes in GC levels. Desert living baboons, for example, have been found to experience drastic changes in core body temperature of up to 5°C and seem to adapt their drinking and other thermoregulatory behaviour accordingly (Brain and Mitchell, 1999). Additionally, individuals might choose to avoid or face the sun depending on the season (Pochron, 2000). Thermoregulatory behaviours are also important for dealing with the cold, for example through huddling (Campbell et al., 2018) or through choice of sleep sites (Barrett et al., 2004).

Besides thermoregulation, weather and season can also influence individuals via availability of food or the quality thereof. Climate and weather are known to influence food availability and vegetation structure (Hill and Dunbar, 2002). As an example, in the Drakensberg, a South African mountain range, winter was found to be connected with lower quality food (Byrne et al., 1993), which might also influence day travel routes and thus energy expenditure. The quality or availability of food, in turn, can be linked to the time animals spend feeding, with baboons spending more time feeding if the proportion of fruit in the diet is low and proportion of subterranean items is high (Hill and Dunbar, 2002). These changes in food availability, weather, season and day length have been found to influence animals' activity budgets (Hill et al., 2003, 2004). For example, baboons were found to be more sedentary with higher temperatures (Hill, 2006) and to spend more time feeding in winter (Byrne et al., 1993). A mostly unappreciated point is that season might also influence social relationships, as was shown in baboons (Henzi et al., 2009).

In baboons, a number of studies have investigated weather effects on GC levels specifically (e.g. chacma baboons [*Papio ursinus*; Weingrill et al., 2004]; olive baboons [*Papio anubis*; MacLarnon et al., 2015]; yellow baboons [*Papio cynocephalus*; Gesquiere et al., 2008; Gesquiere et al., 2011b]), while other studies have incorporated or checked for effects of weather or season on GC levels, but results are highly variable. There was no effect of temperature on fGCM levels in some studies (yellow baboons, Gesquiere et al., 2011b) but a positive correlation of fGCM to temperature in others (yellow baboons, Gesquiere et al., 2008; Gesquiere et al., 2011a; olive baboons, MacLarnon et al., 2015). In Amboseli, male baboons showed elevated GC concentrations if temperature rose above 34°C (Beehner et al., 2006). There was an effect of season on fGCM concentrations in some studies of yellow baboons (Gesquiere et al., 2008; Gesquiere et al., 2011b) and chacma baboons (Kalbitzer et al., 2015), but no effect of seasonality on chacma baboons' fGCM levels in other studies (Bergman et al., 2005; Engh et al., 2006a; Crockford et al., 2008). One study on female chacma baboons found a negative correlation between fGCM levels and daylight duration (Weingrill et al., 2004), and while most studies report no link between fGCM levels and rainfall in baboons (e.g. chacma baboons, Weingrill et al., 2004; olive baboons, Fourie et al., 2015), a study in olive baboons found high rates of rainfall and high humidity to be positively associated with high fGCM concentrations, likely linked to thermoregulatory stress (MacLarnon et al., 2015).

The effect that weather, and its related environmental factors, can have on physiological stress response levels in baboons seems therefore highly variable, and could depend on species and/or habitat type. Therefore, this study investigates the effect that temperature and rainfall have on chacma baboons' fGCM levels. Hereby, this study aims to provide some more evidence on the link, or absence thereof, between weather and physiological stress response levels in baboons and investigates this specifically for a population in a highly seasonal, montane environment.

Predation

Predator attacks are one of the main causes of mortality for many wild animals (Cheney et al., 2006) and predation risk has been argued to be the reason for group living in baboon species (Bettridge and Dunbar, 2012). The systematic study of the effects that predation has on wild non-human primates is difficult, however, due to its inherently unpredictable nature. Some studies have investigated predator-prey interactions (e.g. Bidner et al., 2018) and the effect that group composition has on these interactions (Cowlishaw, 1994; Cheney et al., 2012), and others have looked at behavioural responses of animals towards a dead conspecific (Buhl et al., 2012) or at individual spatial position in the group in the context of predation risk (Tkaczynski et al., 2014). Few studies, though, have investigated the effect that a predation event has on the remaining troop members.

Only one study to my knowledge has looked systematically at physiological and behavioural consequences of predation in a wild troop of non-human primates. Engh et al. (2006a) found in their study on female chacma baboons (*Papio ursinus*) in the Okavango Delta, Botswana, that females who lost a close relative had increased fGCM levels in the four weeks after the predation event compared to the four weeks before the attack, while there was no such increase for matched females that did not lose a close relative. This increase seemed to be of transient nature, however, as fGCM levels in the second month after predation did not differ from the baseline levels. Additionally, while these females lost an important grooming partner, they seemed to adapt their affiliative behaviour after the loss in that they diversified their grooming interactions, groomed more partners, and spent more time overall grooming compared to before. These changes in behaviour were interpreted as helping the individual cope with the loss and thus mitigating their physiological stress response (Engh et al., 2006a). While predation events are much rarer in the Soutpansberg mountains compared to the Okavango Delta, predation by leopards was still assumed to be one of the major stressors baboons experience there, as leopards and brown hyaenas are resident large carnivore species that prey on baboons (Williams et al., 2018). Indeed, while observed predation events were low in the years before the study period, so were mortality rates, and it seems likely that most individuals that disappeared during or shortly after the study period were killed by a predator, as individuals that are injured or ill or weakened for some other reason are generally the most likely to be preyed upon.

Thus, as a basis for the further investigation into differences in stress resilience, the effect of predation on individuals' physiological stress response levels will be investigated here.

3.1.3 Hypotheses and predictions

Based on this prior research, the following hypotheses will be tested using the stated predictions:

Hypothesis 1: Individuals differ in their mean physiological stress response levels and stress reactivity and this variation is linked to demographic factors.

Prediction 1i: Individuals differ in their mean fGCM concentrations.

Prediction 1ii: Mean fGCM concentrations and demonstrated reactive scope differ between the sexes.

Prediction 1iii: Mean fGCM concentrations and demonstrated reactive scope differ between age classes.

Prediction 1iv: Female fGCM concentrations vary with reproductive state.

Prediction 1v: Mean fGCM concentrations and demonstrated reactive scope are linked to dominance hierarchy position.

Hypothesis 2: Ecological factors influence physiological stress response levels.

Prediction 2i: fGCM concentrations are influenced by climatic variation.

Prediction 2ii: fGCM concentrations increase after a predation event.

3.2 Methods

3.2.1 Faecal glucocorticoid metabolite concentrations and DRS

Procedures for faecal sample collection, storage, and processing are described in detail in chapter 2, section 2.2.3. fGCM concentrations of single faecal samples were used in the analysis of inter-individual differences in fGCM levels, in the link between reproductive state and fGCM levels of females, as well as regarding the effect that environmental factors such as weather and predation had on fGCM concentrations (males n = 12, females n = 22, but varying for the predation analysis). In some of these analyses, fGCM values had to be $\log_{10}$-transformed to comply with the assumptions of linear models, but details on this are given with the respective results. Additionally, monthly mean fGCM concentrations were also used to assess inter-individual differences in fGCM concentrations, which are shown in Figure 3.1 and Figure 3.2.

Based on the monthly means, overall mean fGCM concentrations, DRS, and DRS_{CV} values were calculated for all individuals for which samples of at least four months were available (males n = 11, females n = 19), so that a comparative analysis of mean physiological stress response levels and demonstrated reactive scope was possible. These three physiological stress response measures were analysed regarding differences between the sexes, the effect of age, and their link to dominance rank position. While mean fGCM values were normally distributed, DRS and DRS_{CV} values were not and were therefore log_2-transformed if needed to comply with model assumptions, but details on this are given with the results. Demonstrated reactive scope and its coefficient of variation were calculated as described in chapter 2, section 2.2.3.2.

3.2.2 Demographic factors

Age classes were assessed at the beginning of the study period. Females were categorised as either young, middle, or old adults, while males were classed as adolescents, or young, middle, or old adults. For details on group composition and age categories see chapter2, section 2.2.1.

For the comparison of fGCM concentration between reproductive states, females' reproductive state was assessed at the beginning of each observation as either cycling, pregnant, or lactating. To get as exact dates of pregnancy as possible, the potential beginning of pregnancy was calculated backwards from date of giving birth based on a gestation period of ca. 177 days, i.e. just less than 6 months (Beehner et al., 2006), and dates were then matched with *ad libitum* data on swelling sizes and consortships. This way, the females' last known days of mating were still considered as cycling and the female was considered pregnant at the next observation day.

For details on dominance rank calculations see chapter 2, section 2.2.2.2. Here, the association between dominance rank position and mean fGCM concentrations or demonstrated reactive scope was investigated, using both rank categories and continuous mean randomised Elo-ratings. Mean randomised Elo-ratings and rank categories were assessed comparably in separate models and, based on those results, rank category was used in subsequent models as correction term, as will be described further in the results section under prediction 1v.

3.2.3 Environmental factors

To investigate the effect of weather on fGCM concentrations, data from the weather sensor stationed at Lajuma research centre, which is described in detail in chapter 2, section 2.1.2.3, were used. Here, for each day the minimum and maximum temperatures as well as the daily rainfall (in mm) were selected, and additionally the monthly rainfall in mm calculated as a more general measure of seasonal change. When the whole study period was considered, there was a strong positive correlation between daily minimum temperature and monthly rainfall (Spearman rank correlation, S = 1876900, rho = 0.7, $p < .0001$), but this correlation disappeared when only days were considered for which faecal samples were available for either sex (all $r < 0.6$, all $p < .0001$, females: n = 214, males: n = 131). There were no strong correlations above the set threshold of 0.6 among the remaining weather variables (i.e. all $r < 0.6$, all $p < .001$) when considering the whole study period. However, when only considering days for which faecal samples of males were available, maximum and minimum daily temperatures were highly correlated (Pearson’s product-moment correlation, t(129) = 8.75, r = 0.61, $p < .0001$, CI = 0.51, 1.00, n = 131), while there were no high correlations among the other weather variables for either males or females (all $r < 0.6$, $.882 \geq p < .0001$, females: n = 214, males: n = 131). Therefore, effects of maximum and minimum daily temperatures were assessed in separate models, while the other weather variables were included in each model, as indicated with the results.

In addition to the above mentioned weather variables, humidity could potentially also be linked to GC concentrations, as high humidity has been shown to be linked to high rates of self-directed behaviours, such as scratching, in another non-human primate species (Japanese macaques [*Macaca fuscata*; Ventura et al., 2005]).

However, in that study, high humidity was associated with high temperatures, which probably together explained high rates of self-directed behaviour, e.g. due to sweating or higher ectoparasite load, while here humidity was strongly negatively correlated with daily maximum temperature when considering days for which faecal samples were available, i.e. humidity was high when temperatures were low (Spearman's rank correlation, S = 11243000, rho = -0.64, p < .0001, n = 356). Due to this strong correlation and as there was no clear prediction as to how fGCM concentrations would be linked to levels of humidity, humidity was not included in this analysis. When interpreting the results, though, it should be considered that high fGCM concentrations linked to thermoregulatory challenges posed by cold temperatures might be intensified by simultaneously high humidity.

Regarding the analysis of predation, more details on how time periods for hormonal comparisons were selected and the ways in which fGCM data were analysed in this context are given in section 3.3.2.

3.2.4 Statistical analysis

For the analysis of inter-individual differences in fGCM concentrations and for the analysis of differences in physiological stress response measures between age classes, ANOVAs were used and, subsequently, Tukey multiple comparison of means post-hoc tests conducted for pairwise comparison of subsets. Regarding the comparison of physiological stress response measures between the sexes, two-tailed t-tests were conducted, and for an investigation into the change of fGCM concentrations after predation events compared to baseline levels, paired two-tailed t-tests were used. If data were not normally distributed, log-transformations ($\log_2$ or $\log_{10}$) were used to transform them to normality. Where possible, 95%-CIs are reported.

For an analysis of the effects of reproductive state and environmental factors on fGCM concentrations, as well as of the link between mean fGCM levels, DRS, and DRS_{CV} and dominance rank position, LMs or LMMs were used. Details on fixed and random effects of full models are reported with the results. Tables give an overview of the model comparison results, including Δ AIC_C and marginal effect sizes [%] of all models, while full details of all models are collected in Appendix III. Details on the modelling procedure and on the model selection approach used, as well as on the way data are visualised, are given in chapter 2, section 2.3.

3.3 Results

3.3.1 Demographic factors

Hypothesis 1: Individuals differ in their mean physiological stress response levels and stress reactivity and this variation is linked to demographic factors.

Prediction 1i: Individuals differ in their mean fGCM concentrations.

To investigate inter-individual variation in fGCM concentrations, both single faecal sample fGCM concentrations and monthly means had to be $\log_{10}$-transformed to be normally distributed. While individuals differed in their fGCM levels when single sample values were used (ANOVA, F(33, 311) = 2.45, $p < .001$; n = 30), they did not when comparing mean monthly fGCM concentrations, on which further calculation of mean fGCM concentrations and demonstrated reactive scope were based (ANOVA, F(29, 149) = 1.11, p = .331). When the sexes were analysed separately, there was only a trend for inter-individual variation of males' sample fGCM concentrations (ANOVA, F(11, 119) = 1.75, p = .07; n = 11), and no significant difference between males in their mean monthly fGCM concentrations (ANOVA, F(10, 53) = 1.47, p = .177; Figure 3.1). For females, there was significant inter-individual variation in their sample fGCM concentrations (ANOVA, F(21, 192) = 2.65, p < .001; n = 19), but also not in their mean monthly fGCM levels (ANOVA, F(18, 96) = 2.65, p = .393; Figure 3.2).

While statistical analysis of inter-individual differences in DRS and DRS_{CV} are not possible with only one value per individual, the graphical representation of the demonstrated reactive scope measures of males (Figure 3.3) and females (Figure 3.4) suggests that there might be meaningful variation between individuals.

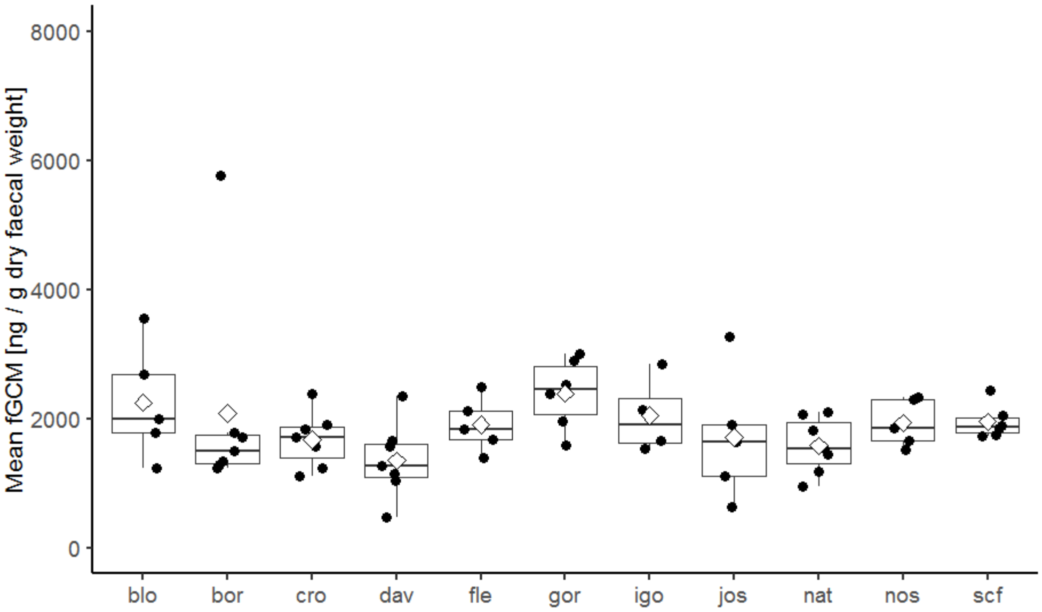


Figure 3.1 Mean fGCM concentrations [ng/g dry faecal weight] of males (n = 11), with individuals arranged in alphabetical order. Black points represent the monthly means, white diamonds depict the overall mean based on the monthly means. Boxes show IQR, vertical line notes median, and whiskers go out to furthest point within 1.5x IQR.

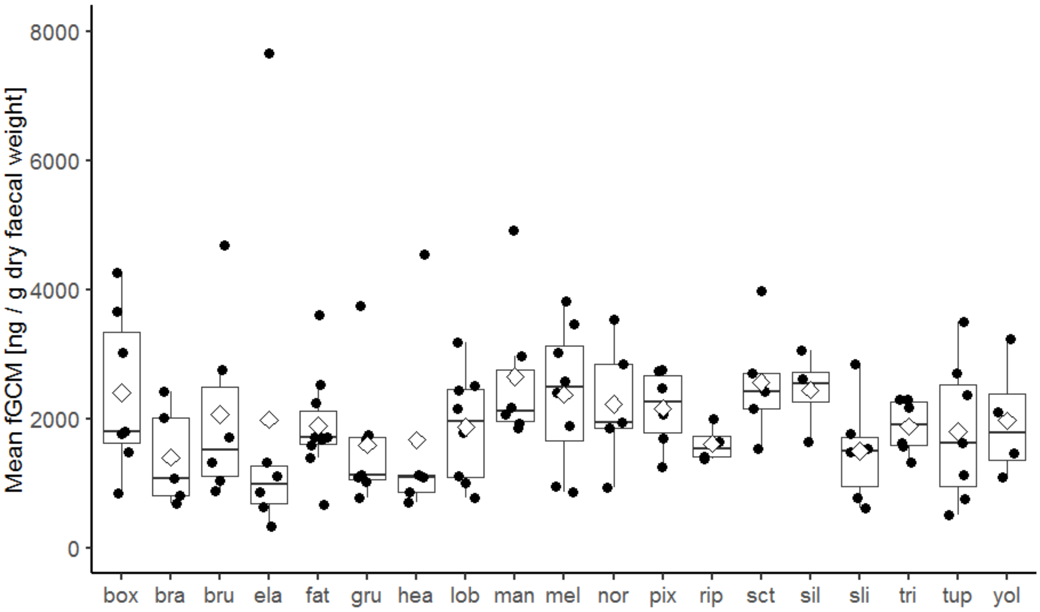


Figure 3.2 Mean fGCM concentrations [ng/g dry faecal weight] of females (n = 19), with individuals arranged in alphabetical order. Black points represent the monthly means, white diamonds depict the overall mean based on the monthly means. Boxes show IQR, vertical line notes median, and whiskers go out to furthest point within 1.5x IQR.

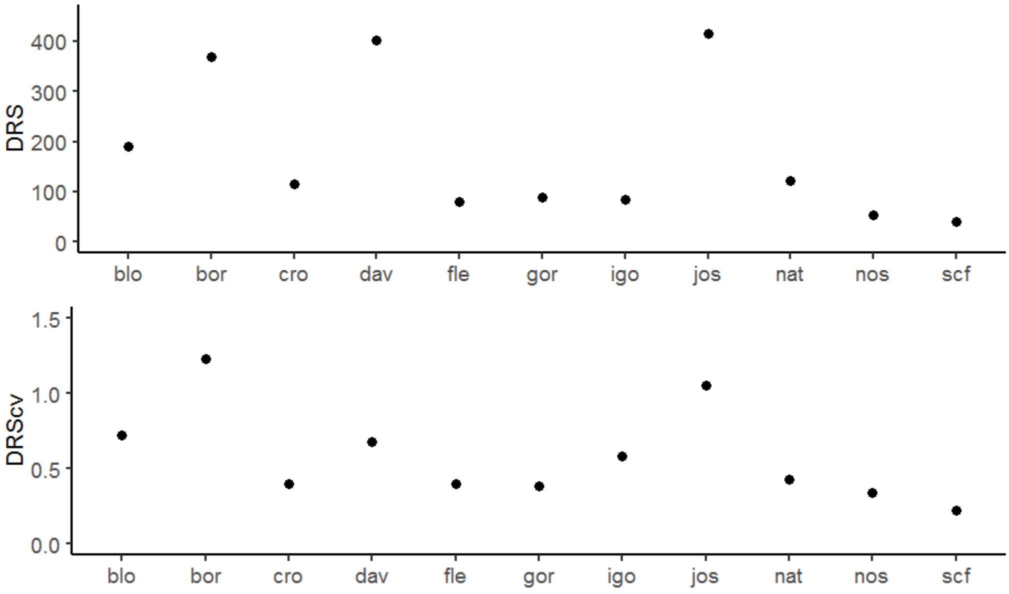


Figure 3.3 Demonstrated reactive scope measured as DRS (top) and DRS$_{CV}$ (bottom) of males (n = 11), with individuals arranged in alphabetical order. The three individuals with very high DRS (bor, dav, jos) were lower-ranking males, which were either of older age (dav, jos) or young but had sustained a severe injury during the study period (bor).

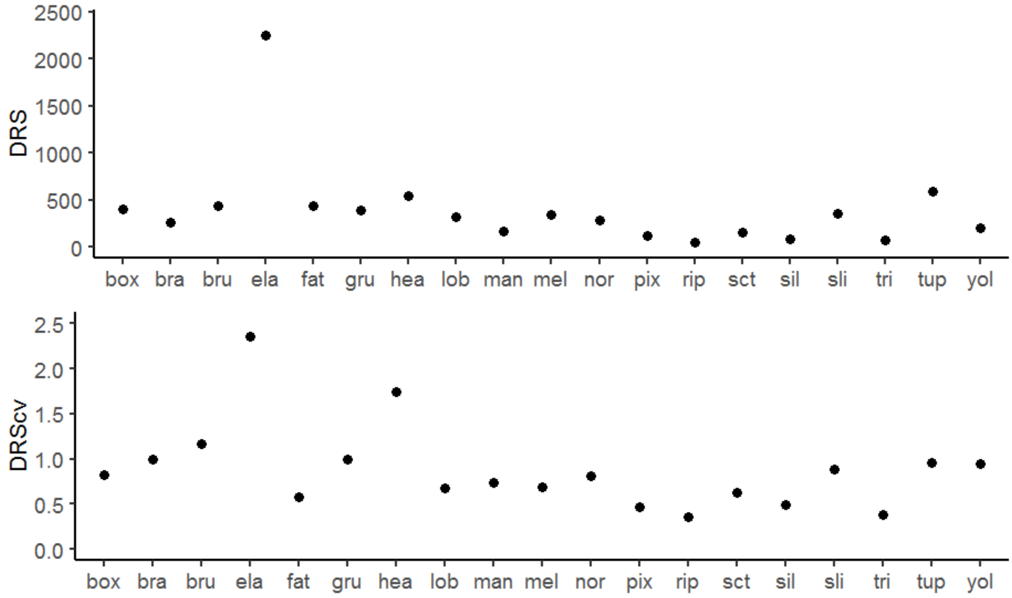


Figure 3.4 Demonstrated reactive scope measured as DRS (top) and DRS_{CV} (bottom) of females (n = 19), with individuals arranged in alphabetical order. The individual with very high DRS (ela) was a high-ranking, old adult female, with the highest measured monthly mean fGCM concentration just before parturition, and also lowest measured monthly mean, resulting in very high demonstrated reactive scope.

Prediction 1ii: Mean fGCM concentrations and demonstrated reactive scope differ between the sexes.

While mean fGCM concentrations were normally distributed, DRS and DRS_{CV} values were not and were therefore $\log_2$-transformed to comply with parametric test assumptions. Males and females did not differ in their mean fGCM levels (t-test, t(24) = -0.83, p = .41, CI = -358.48, 152.2), but females showed higher demonstrated reactive scope than males, both measured as DRS (t-test, t(22.4) = -2.2, p = .039, CI = -1.95, -0.06) and DRS_{CV} (t-test, t(19.6) = -2.21, p = .039, CI = -1.17, -0.03). Additionally, females had a wider range than males of both DRS (min – max ≙ range: females 45.92 – 2254.51 ≙ 2208.59; males 40.13 – 414.39 ≙ 374.26) and DRS_{CV} (min – max ≙ range: females 0.36 – 2.36 ≙ 2.00; males 0.22 – 1.23 ≙ 1.01) as depicted in Figure 3.5. These results hold true if the female outlier is removed, as there was still a statistical trend towards a difference for DRS (t-test, t(19.5) = -1.93, p = .068, CI = -1.74, 0.07) and DRS_{CV} (t-test, t(17.5) = -1.97, p = .065, CI = -1.06, 0.04), and females still had a wider range of DRS (min – max ≙ range: females 45.92 – 589.80 ≙ 543.88; males 40.13 – 414.39 ≙ 374.26) and DRS_{CV} (min – max ≙ range: females 0.36 – 1.74 ≙ 1.38; males 0.22 – 1.23 ≙ 1.01). Consequently, all further analyses were done on males and females separately.

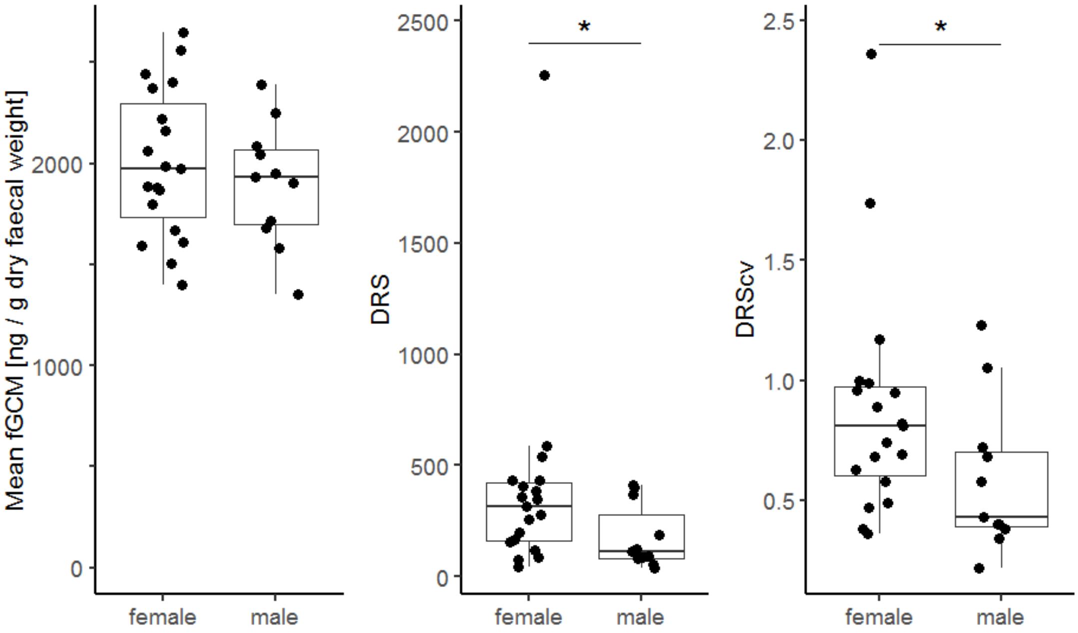


Figure 3.5 Males’ and females’ mean physiological stress response levels, measured as mean fGCM concentrations [ng/g dry faecal weight] on the left, and their demonstrated reactive scope, measured as DRS in the middle and measured as DRS_{CV} in the right graph. Males: n = 11, females: n = 19; DRS and DRS_{CV} values were $\log_2$-transformed in analyses but raw data are presented here; asterisks indicate significance level: * $p < .05$ (t-tests, mean fGCM: t(24) = -0.83, p = .41, CI = -358.48, 152.2; DRS: t(22.4) = -2.2, p = .039, CI = -1.95, -0.06; DRS_{CV}: t(19.6) = -2.21, p = .039, CI = -1.17, -0.03).

Prediction 1iii: Mean fGCM concentrations and demonstrated reactive scope differ between age classes.

As before, males’ DRS and DRS_{CV} values were $\log_2$-transformed to comply with parametric test assumptions. Their physiological stress response measures by age classes are shown in Figure 3.6. The mean fGCM levels of males varied over different age classes (ANOVA, F(3,7) = 8.5, p = .009), with young males having higher mean fGCM levels than both adolescents (post hoc Tukey test, est. = 470.91, p = .031, CI = 49.30, 892.51) and old males (post hoc Tukey test, est. = 659.77, p = .011, CI = 181.71, 1137.82).

There was no statistical evidence for differences in mean fGCM concentrations between other age classes.

The demonstrated reactive scope measured as DRS also varied by age classes for males (ANOVA, F(3, 7) = 7.33, p = .015). DRS of old individuals was significantly higher than of middle-aged ones (post hoc Tukey test, est. = 3.15, p = .011, CI = 0.86, 5.43). There was no statistical difference between the other age categories. While DRS_{CV} also varied significantly across age classes (ANOVA, F(3, 7) = 4.39, p = .049), post-hoc tests revealed no statistically significant differences between means of age classes.

For females, DRS and DRS_{CV} scores were also log_2-transformed, and their physiological stress response measures across age classes are depicted in Figure 3.7. As for males, mean fGCM values differed across age classes for females (ANOVA, F(2, 16) = 4.40, p = .03) with post-hoc tests revealing that old females had lower mean fGCM levels than middle-aged females (post hoc Tukey test, est. = -540.15, p = .024, CI = -1013.08, -67.22), while there were no statistical differences between the other age classes.

In contrast to males, demonstrated reactive scope did not vary across age classes for females (ANOVA, DRS: F(2, 16) = 0.46, p = .624; DRS_{CV}: F(2, 16) = 0.87, p = .439).

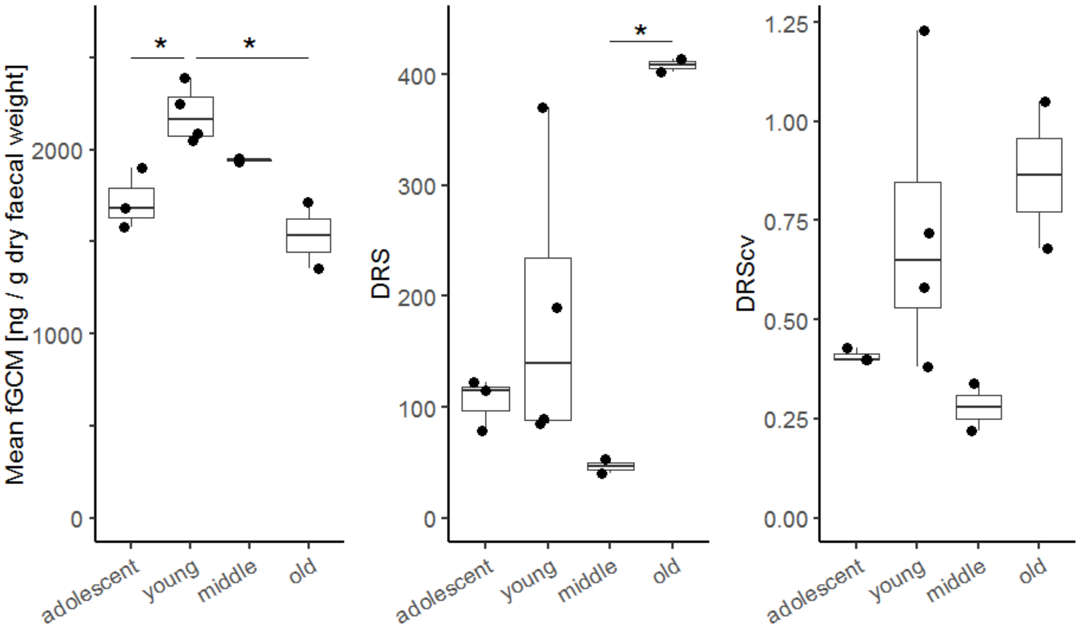


Figure 3.6 Males' physiological stress response measures by age classes, with their mean fGCM concentrations [ng/g dry faecal weight] in the left graph and their demonstrated reactive scope measured as DRS in the middle and DRS_{CV} in the right graph. DRS and DRS_{CV} values were $\log_2$-transformed in analyses but raw data are presented here; asterisks indicate significance level: * $p < .05$ (ANOVAs, mean fGCM: $F(3,7) = 8.5$, $p = .009$; DRS: $F(3, 7) = 7.33$, $p = .015$; DRS_{CV}: $F(3, 7) = 4.39$, $p = .049$).

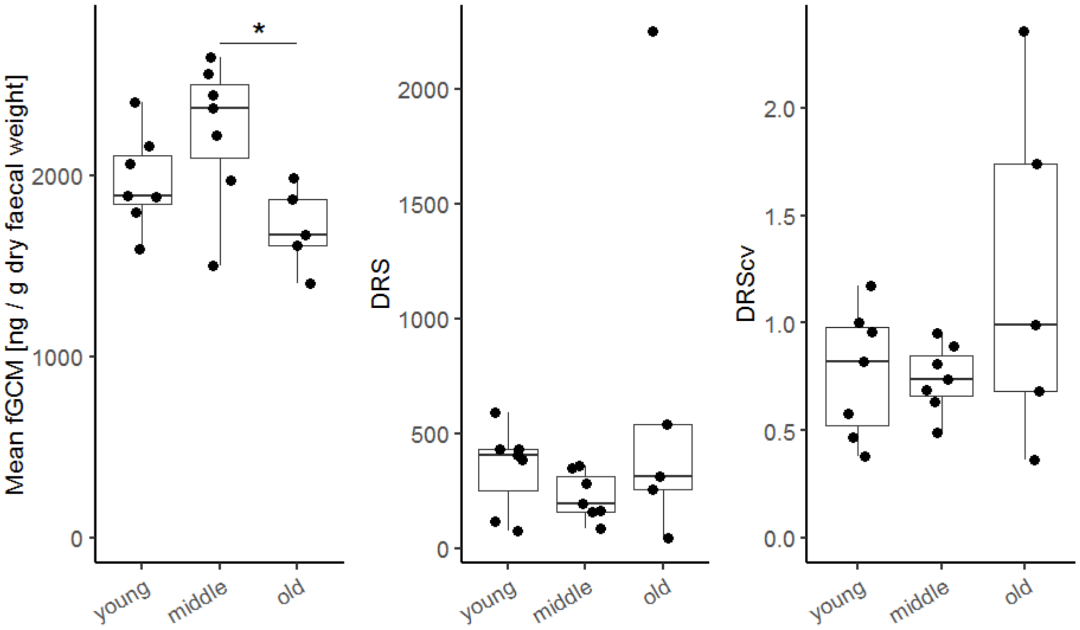


Figure 3.7 Females' physiological stress response measures by age classes, with their mean fGCM concentrations [ng/g dry faecal weight] in the left graph and their demonstrated reactive scope measured as DRS in the middle and DRS_{CV} in the right graph. DRS and DRS_{CV} values were $\log_2$-transformed in analyses but raw data are presented here; asterisks indicate significance level: * $p < .05$ (ANOVAs, mean fGCM: $F(2, 16) = 4.40$, $p = .03$; DRS: $F(2, 16) = 0.46$, $p = .624$; DRS_{CV}: $F(2, 16) = 0.87$, $p = .439$).

Prediction 1iv: Female fGCM concentrations vary with reproductive state.

To investigate if females' reproductive state was linked to their physiological stress response measures, a LMM was constructed including their reproductive state at the time of sample collection and compared to a null model. Both the full and the null model included weather variables as fixed effects as these were shown elsewhere to influence fGCM measurements (prediction 2i), as well as age and rank category. fGCM concentrations were $\log_{10}$-transformed to assure compliance with linear model assumptions.

Females' fGCM levels were linked to their reproductive state as the model comparison shows (Table 3.1). fGCM concentrations were significantly lower during lactation compared to cycling or pregnancy, but there was no difference between the latter two states (Appendix III-I; Figure 3.8). The full model had a substantially better fit as the null model had a Δ $AIC_C > 2$. Additionally, the marginal effect size was by about 6% larger for the full model.

Pairwise plotting was not possible for a comparison of lactation to cycling due to the long lactation period and thus few females that occurred in both of these reproductive states. While sample fGCM concentrations were used for analysis, figures show mean fGCM concentrations of females during specific reproductive states (Figure 3.8). Due to the limited number of faecal samples, it was also not possible to compare demonstrated reactive scope measures of females in different reproductive states.

LMM: *log_{10}(fGCM) ~ reproductive state + max. temperature + rain/day + rain/month + age + rank + (1|individual)*

Table 3.1 Results of the LMM comparisons regarding females' fGCM concentrations during different reproductive states. The full model included reproductive state as a factor, and all models included age, rank category and weather variables, as well as ID as random factor. Models with a Δ AIC_C < 2 were considered to have received substantial support and are marked in bold and underlined.

	Response variable: (Δ AIC_C, marginal R^2 [%])	
	fGCM	
Predictor:	**Δ AIC_C**	**R^2**
reproductive state	**<u>0</u>**	**<u>14.37</u>**
null model	5.05	8.18

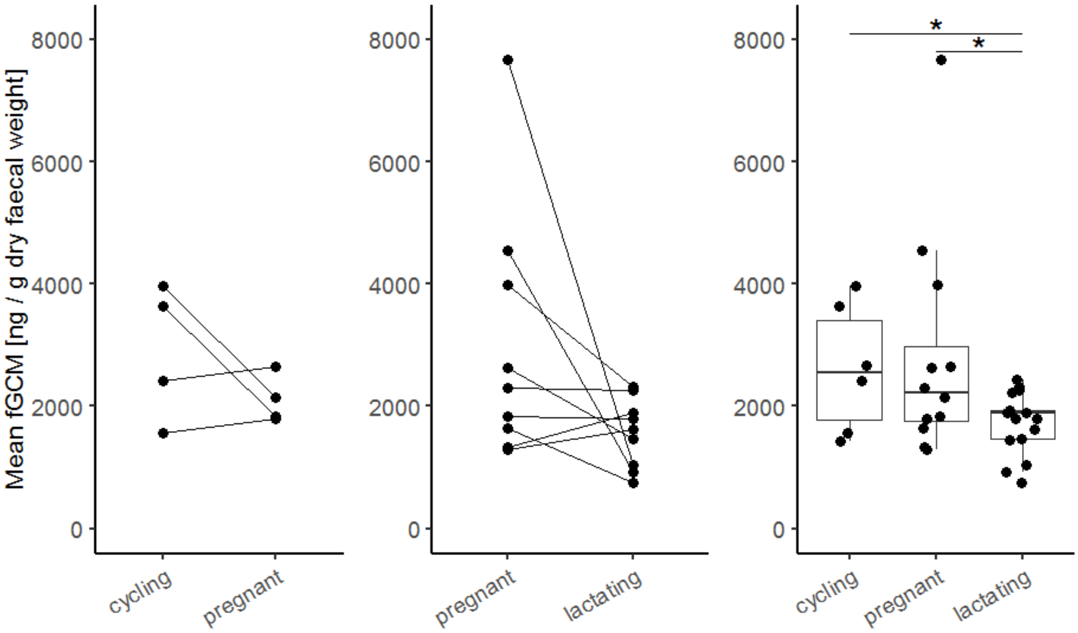


Figure 3.8 Mean fGCM concentrations [ng/g dry faecal weight] of females: paired data of cycling and pregnant females (n = 4, left); paired data of pregnant and lactating females (n = 9, middle); all females included based on their reproductive state at the time of faecal sample collection (n = 22, right). fGCM concentrations were log_{10}-transformed in analysis but raw data are presented here; asterisks indicate significance level: * $p < .05$ (Δ AIC_C = 0 and R^2 = 14.73%).

Prediction 1v: Mean fGCM concentrations and demonstrated reactive scope are linked to dominance hierarchy position.

To investigate whether physiological stress response measures were linked to dominance rank position, LMs were constructed using either rank category or mean randomised Elo-rating as fixed effect, thus assessing the link between rank and mean fGCM concentrations as well as demonstrated reactive scope, measured as DRS and

DRS_{CV}. Age was included as fixed factor and kept in the null model. Results of the model comparison are shown in Table 3.2, while details of the full model can be found in Appendix III-I. Age was not correlated with rank category for either males (LM, $F(1,9) = 2.44$, $p = .153$) or females (LM, $F(1,17) = 0.4$, $p = .537$), nor with the mean randomised Elo-ratings of males (LM, $F(1,9) = 1.60$, $p = .237$) or females (LM, $F(1,17) = 0.58$, $p = .457$).

For males, full models including rank category or mean randomised Elo-ratings only received weak support towards a link to individuals' mean physiological stress response levels measured as mean fGCM concentration. While Δ AIC_C of the full model including rank category was 2.82, the full model's effect size was about 15% larger than the null model effect size, explaining about 20% of variation in males' mean fGCM concentrations (Figure 3.9). There was no support for a link between dominance rank position and demonstrated reactive scope either measured as DRS or DRS_{CV} based on the model comparisons.

For females, the full model including rank category received substantial support in explaining mean fGCM variation, as both the full model including mean randomised Elo-ratings and the null model had Δ $AIC_C > 2$ (Figure 3.10). Effect sizes of full models were considerably larger than that of the null model, with 38% and 31% compared to 5% seen with the null model. When investigating the link between dominance rank and demonstrated reactive scope, the DRS values of females had to be $\log_2$-transformed to assure compliance with linear model assumptions, and DRS_{CV} values were also $\log_2$-transformed, though not strictly necessary, to maintain comparability to other analyses. There was no support for a link between either measure of rank and DRS or DRS_{CV} based on model comparisons, and in both cases the null models were at least five times as likely to be the best model of the set of models.

As the models including rank category were able to explain more variation in mean fGCM concentrations in both males and females than the models including individuals' mean randomised Elo-ratings, rank categories were used as control factors in all subsequent models.

LM: *stress measure ~ rank measure + age*

Table 3.2 Results of the LM comparisons regarding the link between males' and females' dominance rank position, measured as rank category or mean randomised Elo-rating, and their physiological stress response measures, i.e. mean fGCM concentration, DRS, and DRS_{CV}. Models included age. Models with a $\Delta \text{AIC}_C < 2$ or strikingly large effect sizes were considered to have received substantial support and are marked in bold and underlined.

	MALES						FEMALES					
	Response variable: (ΔAIC_C, marginal R^2 [%])											
	mean fGCM		**DRS**		**DRS_{CV}**		**mean fGCM**		**DRS**		**DRS_{CV}**	
Predictor:	**ΔAIC_C**	**R^2**	**ΔAIC_C**	**R^2**	**ΔAIC_C**	**R^2**	**ΔAIC_C**	**R^2**	**ΔAIC_C**	**R^2**	**ΔAIC_C**	**R^2**
rank category	**2.82**	**20.99**	3.9	32.80	4.97	9.11	**0**	**37.69**	3.25	0.28	3.14	7.11
rand. Elo-rating	3.33	17.87	3.25	36.18	4.09	14.89	2.12	30.89	3.22	0.42	3.24	6.69
null	**0**	**5.84**	**0**	**27.74**	**0**	**8.11**	5.54	5.17	**0**	**0.29**	**0**	**6.96**

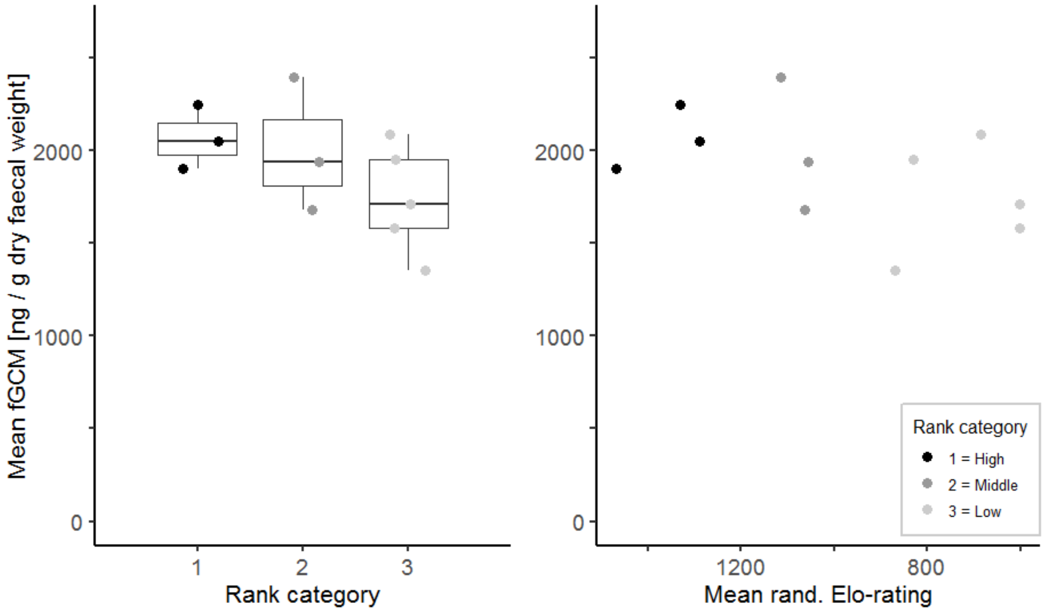


Figure 3.9 Mean fGCM concentrations [ng/g dry faecal weight] of males in relation to their rank category and mean randomised Elo-ratings (n = 11) (rank category: $\Delta \text{AIC}_C = 2.82$ and $R^2 = 20.99\%$; mean randomised Elo-rating: $\Delta \text{AIC}_C = 3.33$ and $R^2 = 17.84\%$).

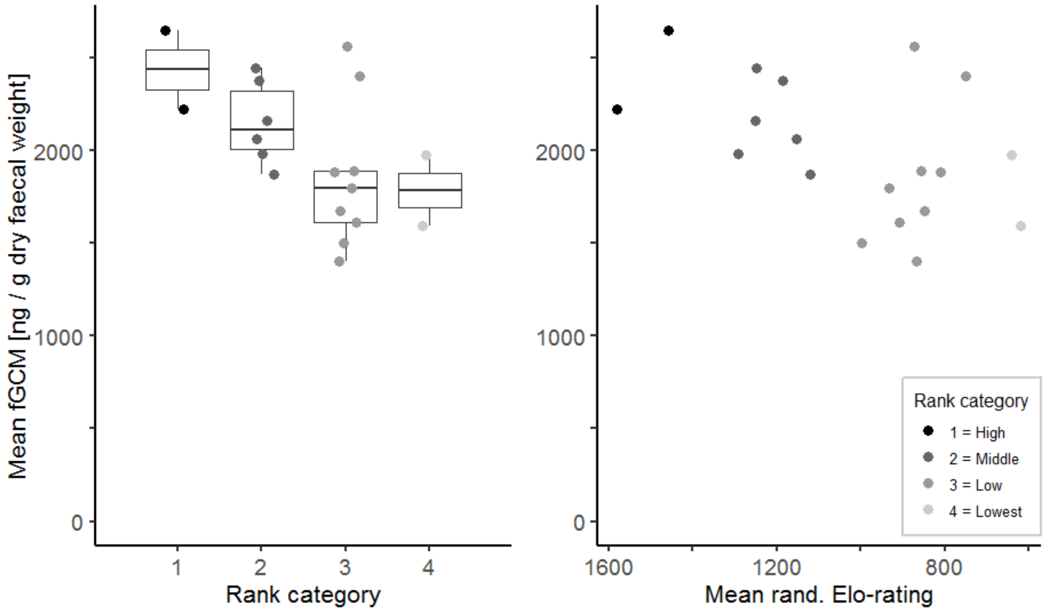


Figure 3.10 Mean fGCM concentrations [ng/g dry faecal weight] of females in relation to their rank category and mean randomised Elo-ratings (n = 19) (rank category: Δ AIC$_C$ = 0 and R^2 = 37.69%; mean randomised Elo-rating: Δ AIC$_C$ = 2.12 and R^2 = 30.89%).

3.3.2 Environmental factors

Hypothesis 2: Ecological factors influence physiological stress response levels.

Prediction 2i: fGCM concentrations are influenced by climatic variation.

Here, it was investigated which of the recorded ecological factors, such as temperature and rainfall, influenced baboons’ fGCM levels. All analyses were done on males and females separately. As described in section 3.2.3, maximum and minimum daily temperatures were highly correlated when considering only the days for which male faecal samples were available, so separate models including either maximum or minimum daily temperatures were constructed for each sex. Besides temperature, the full models also included rainfall/day [mm] and rainfall/month [mm] as fixed effects, as well as age and rank category, and reproductive state for females. Individual ID was included as a random factor. All fGCM values were $\log_{10}$-transformed to assure compliance with assumptions of linear models. An overview of the model comparison results can be found in Table 3.3, while full details of all models are collated in

Appendix III-II.

For males, only the full model including minimum daily temperature received substantial support, with Δ AIC$_C$ > 2 of both the maximum temperature full model and the null model. When assessing the importance of single predictors, only temperature was a significant predictor, while there was no significant effect of rainfall per day or rainfall per month (see Appendix III-II). Minimum temperature was negatively associated with fGCM concentrations in males, i.e. males had higher fGCM levels when minimum temperatures were lower (Figure 3.11).

For females, the effect of environmental factors on physiological stress response levels could potentially differ between reproductive states due to, for example, differences in energetic demands or differences in the females' tolerance of heat or cold. Therefore, in addition to the full models constructed comparably to males, full models including an interaction term of reproductive state and weather variables were calculated. In all weather models, however, only temperature seemed to be linked to any individual's fGCM levels. Therefore, and to keep model parameters to a minimum to avoid over-fitting, interaction terms of daily temperature and reproductive state were included, but no interaction of reproductive state and rainfall. These 'interaction models' were compared to full models containing the same parameters minus the interaction term, as well as a null model without any weather variables.

The full model including maximum daily temperature and no interaction term was the best model of the set, with Δ AIC$_C$ > 2 of all other models. Based on the full model details, maximum daily temperature negatively predicted females' fGCM concentrations, in that females had higher fGCM levels when maximum daily temperatures were low (Figure 3.12). While the interaction models had overall worse fit than the simple maximum temperature model, it is striking that the interaction term of reproductive state and minimum daily temperature was a significant predictor of females' fGCM concentrations. These results indicate that in lactating females, low minimum daily temperatures were connected to higher fGCM concentrations, while cycling and pregnant females had higher fGCM levels when minimum daily temperatures were higher (Figure 3.13).

Overall, weather seemed to influence both males' and females' fGCM levels to certain degrees. While for males, minimum daily temperature was found to be the best predictor of fGCM variation, for females, maximum daily temperature was the best predictor. Interestingly, there was also some support for an interaction effect of minimum daily temperature and reproductive state for females, i.e. lactating females might react differently to changes in minimum daily temperature than cycling or pregnant females do, in addition to the general effect that reproductive state seems to have on females' physiological stress response levels. Across all models, though, low temperatures rather than high temperatures were connected to higher fGCM concentrations, indicating that baboons at the study site had to spend energy on thermoregulatory processes to cope with the cold.

Male LMM: log_{10} *(fGCM) ~ temperature measure + rain/day + rain/month + age + rank category + (1|individual)*

Female LMM: log_{10} *(fGCM) ~ temperature measure + reproductive state + rain/day + rain/month + age + rank category + (1|individual)*

Fem. inter. LMM: log_{10} *(fGCM) ~ temperature measure * reproductive state + rain/day + rain/month + age + rank category + (1|individual)*

Table 3.3 Results of the LMM comparisons regarding the link between males' and females' fGCM concentrations and weather variables, using either maximum or minimum daily temperature as fixed effect as marked, and rain/day and rain/month as fixed effect in all full models. Models included age and rank category, and reproductive state for females. For females, additional interaction models were constructed, including an interaction term of the temperature measure and females' reproductive state. ID was used as random factor. All fGCM concentrations were $\log_{10}$-transformed. Models with a Δ $AIC_C < 2$ were considered to have received substantial support and are marked in bold and underlined.

	MALES		FEMALES	
	Response variable (Δ AIC_C, marginal R^2 [%])			
	fGCM			
Predictor:	**Δ AIC_C**	**R^2**	**Δ AIC_C**	**R^2**
max. temperature	4.55	10.97	**0**	**15.16**
max. temperature * reproductive state			2.51	14.38
min. temperature	**0**	**14.06**	9.17	10.9
min. temperature * reproductive state			3.1	14.82
null	8.74	3.36	6.33	9.43

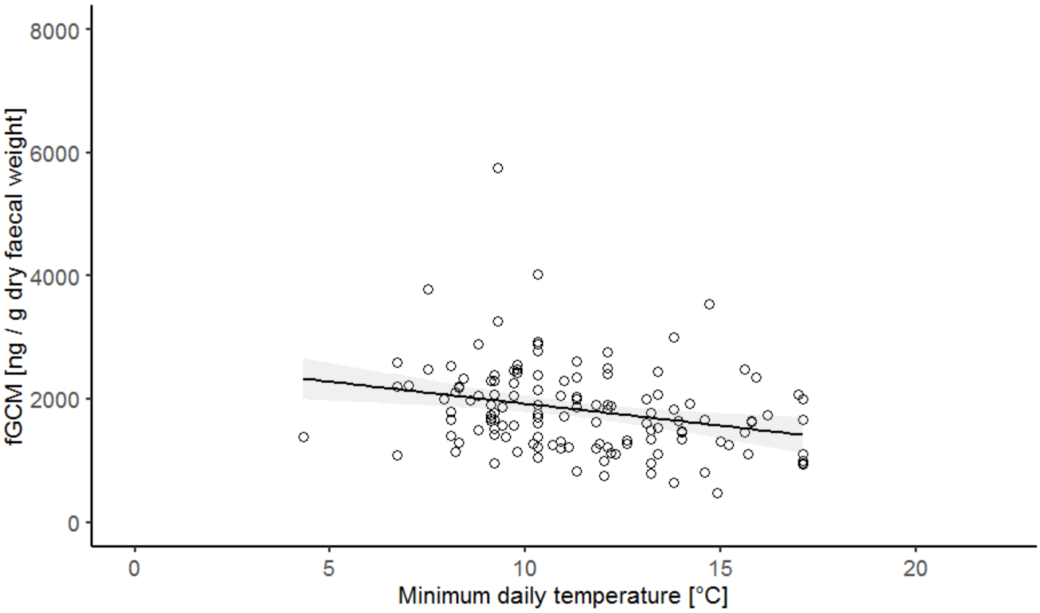


Figure 3.11 Male fGCM concentrations [ng/g dry faecal weight] by minimum daily temperature [°C] (n = 12 individuals). Regression line is based on simple LM of fGCM by minimum daily temperature, with 95%-CI as shaded area. While fGCM values were $\log_{10}$-transformed in the analysis, the y-axis was not transformed here to keep meaningfulness (Δ $AIC_C = 0$ and $R^2 = 14.06\%$).

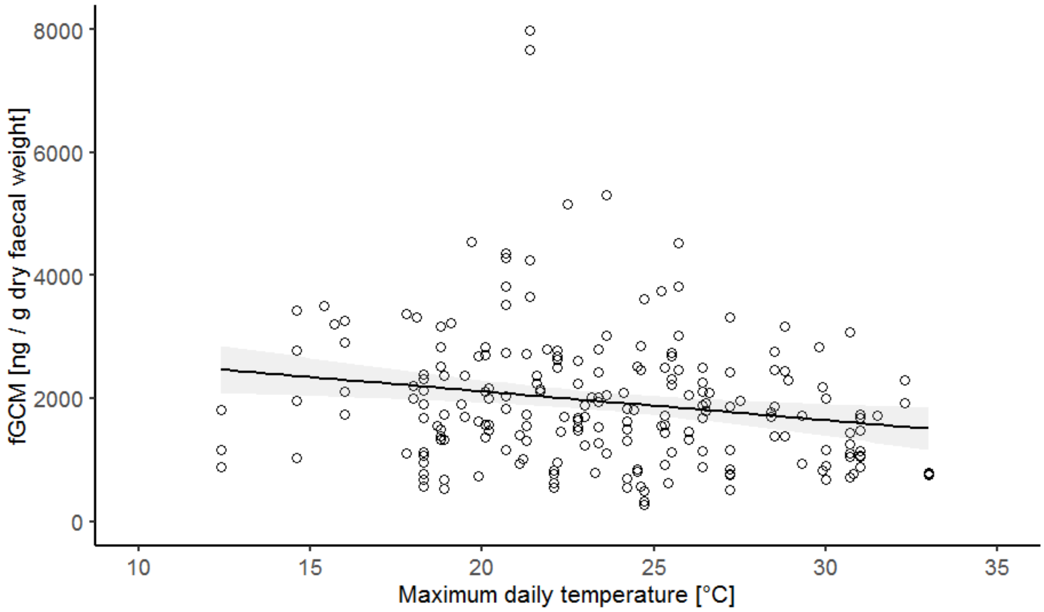


Figure 3.12 Female fGCM concentrations [ng/g dry faecal weight] by maximum daily temperature [°C] (n = 22 individuals). Regression line is based on simple LM of fGCM by maximum daily temperature, with 95%-CI as shaded area. While fGCM values were $\log_{10}$-transformed in the analysis, the y-axis was not transformed here to keep meaningfulness (Δ $AIC_C = 0$ and $R^2 = 14.38\%$).

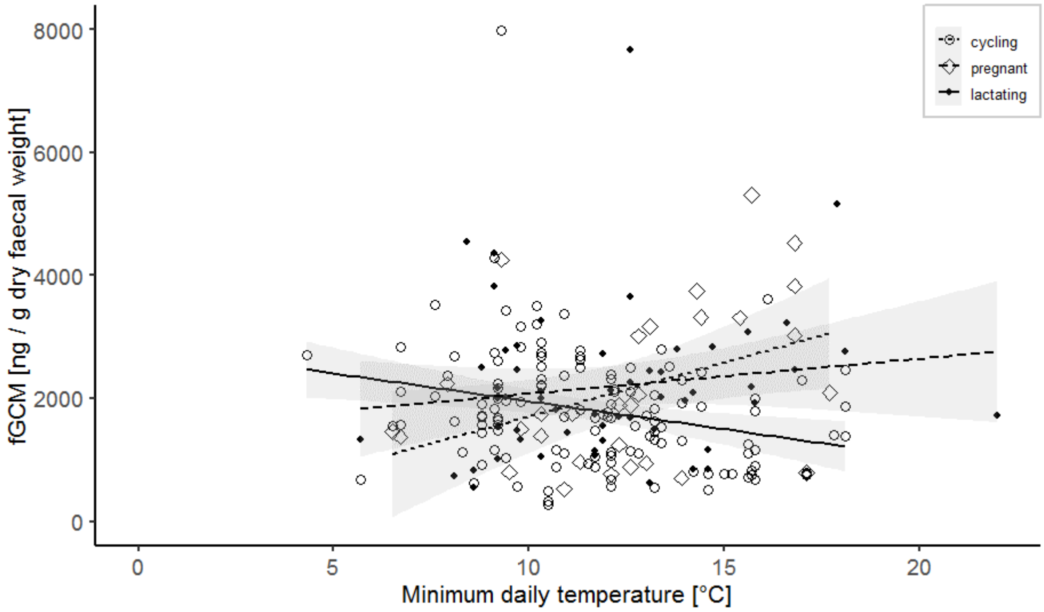


Figure 3.13 Female fGCM concentrations [ng/g faecal weight] by minimum daily temperature [°C] (n = 22 individuals). Shapes and lines represent reproductive states as described in the legend, regression lines are based on simple LM of fGCM by minimum daily temperature of females in the same reproductive state, with 95%-CI as shaded areas. While fGCM values were $\log_{10}$-transformed in the analysis, the y-axis was not transformed here to keep meaningfulness (Δ $AIC_C = 3.1$ and $R^2 = 14.82\%$; interaction term of minimum temperature and reproductive state significant predictor of fGCM variation).

Prediction 2ii: fGCM concentrations increase after a predation event.

To investigate the effect of predation on physiological stress response levels, pre- and post-predation time periods were compared, comparable to the study by Engh et al. (2006a). As there were several deaths and emigrations happening in a short amount of time, it was not possible to differentiate between the effects of all of these. Thus, the time from beginning of June to the end of data collection in November was divided up into four periods, i.e. before and after event period 1, and before and after event period 2. Here, period 1 includes the emigration of an adolescent male and the predation on an adult female (the first recorded predation event on an adult individual in several years), while period 2 pools the emigration of another adolescent male, the disappearance of two adult females, and the observed predation on another adult male (Table 3.4).

Table 3.4 Time periods pre- and post-predation/disappearance and emigration events that are used in the subsequent analysis of the effects of these events on fGCM concentrations of the troop members.

<table>
<tr><td>Month</td><td>June</td><td colspan="2">July</td><td colspan="2">August</td><td colspan="2">September</td><td>October</td><td>November</td></tr>
<tr><td rowspan="2">Time period</td><td colspan="4">Period 1</td><td colspan="5">Period 2</td></tr>
<tr><td colspan="2">before 1
09/06-08/07</td><td colspan="2">after 1
09/07-14/08</td><td colspan="2">before 2
23/08-22/09</td><td colspan="3">after 2
23/09-07/11</td></tr>
<tr><td>Events</td><td colspan="2"></td><td colspan="2">- emigration
<i>fla 08/07</i>
- predation
<i>per 13/07</i></td><td colspan="2"></td><td colspan="2">- emigration
<i>gor ca. 20/09</i>
- disappearance
<i>ste 04/10</i>
<i>sho 05/10</i>
- predation
<i>bor 02/11</i></td><td>- end of data collection
<i>07/11</i></td></tr>
</table>

When comparing before and after mean fGCM concentrations, only individuals for which samples were available during all periods (n = 12) were included, and progression of mean fGCM concentrations are depicted in Figure 3.14. In period 1, mean fGCM concentrations increased from before to after period 1 (paired t-test: t(11) = 5.846, est. = 681.91, p = .0001, CI = 425.18, 938.64), and then decreased significantly from after period 1 to before period 2 (paired t-test: t(11) = -2.492, est. = -437.07, p = .03, CI = -832.12, -51.02). This likely represents the return to baseline levels, as before 1 and before 2 levels did not differ (paired t-test: t(11) = 1.615, est. = 244.84, p = .135, CI = -88.76, 578.45). For period 2, there was no significant difference in means, but a statistical trend towards a decrease of mean fGCM values from before to after (paired t-test: t(11) = -2.192, est. = -342.53, p = .051, CI = -686.48, 1.43).

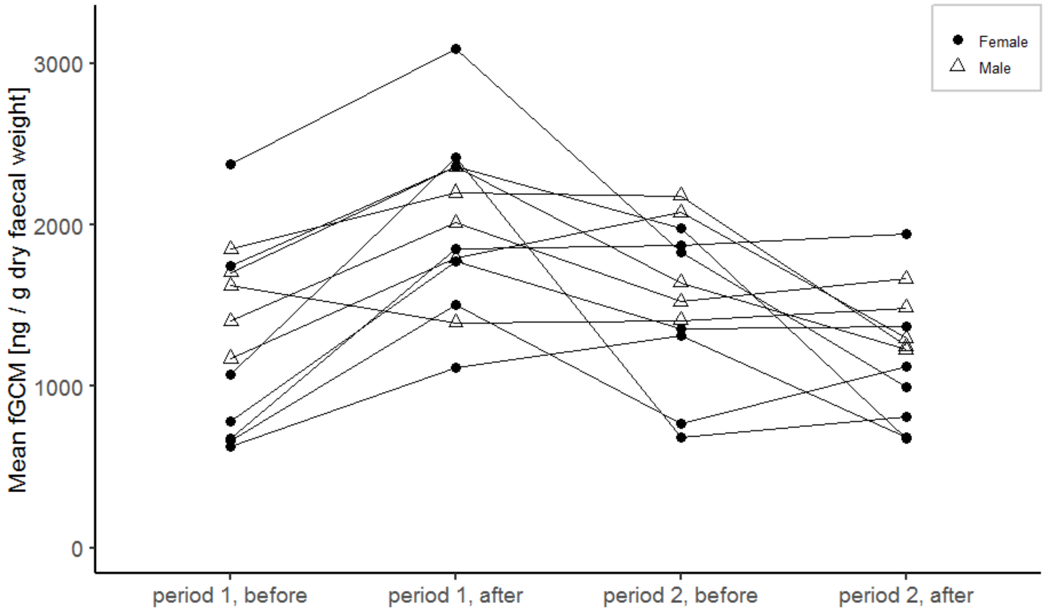


Figure 3.14 Mean fGCM concentrations over two time periods of predation and disappearance events, divided each into a before and after time period (n=12, paired data). Shape marks sex, as shown in the legend.

Change in physiological stress response levels with time

To look for temporal patterns in the change of physiological stress response levels, the change in fGCM as the difference between the 'after' values and the mean 'before' value, i.e. Δ fGCM, was linked to time passed since the first predation or disappearance event of the time period. For both periods, the same 12 individuals were included that were used for the analysis above. In this subset of data, age and sex were highly correlated and age was therefore excluded from the models. Results of the model comparisons are compiled in Table 3.5, while full details of the models are presented in Appendix III-II.

For period 1, there was a decrease of Δ fGCM over time, i.e. the increase in fGCM was highest immediately after the predation and got smaller over the month (Figure 3.15). The full model received substantial support, as the null model had a Δ AIC$_C$ > 2, and the effect size of the full model was with 25.61% larger than the effect size of the null model with 18.41%. The number of days did not come up as a significant predictor of Δ fGCM, but sex was a significant predictor in the full model, i.e. the increase of fGCM concentrations after predation depended on the sex of the individual. This indicates that females had a significantly stronger increase in fGCM concentrations after predation event 1 than males did.

As shown before, fGCM levels generally decreased during time period 2, and thus also the Δ fGCM decreased with time (Figure 3.15). Here, none of the predictors had a singular significant effect on Δ fGCM, but the full model again received substantial support with a Δ AIC$_C$ > 2 of the null model. The full model also had a higher marginal effect size than the null model, i.e. 17.97% compared to 11.56%.

LMM: *Δ fGCM ~ days + rank + sex + (1|individual)*

Table 3.5 Results of the LMM comparisons regarding the link between the number of days since the first event of a ‘predation period’ and the change in fGCM concentrations from the mean level before the predation events, analysed together in males and females. Models included rank category and sex. ID was used as random factor. Models with a Δ AIC$_C$ < 2 were considered to have received substantial support and are marked in bold and underlined.

	Response variable: (Δ AIC$_C$, marginal R^2 [%])			
	Δ fGCM			
	Period 1		Period 2	
Predictor:	**Δ AIC$_C$**	**R^2**	**Δ AIC$_C$**	**R^2**
days	**0**	**25.61**	**0**	**17.97**
null	5.73	18.41	5.33	11.56

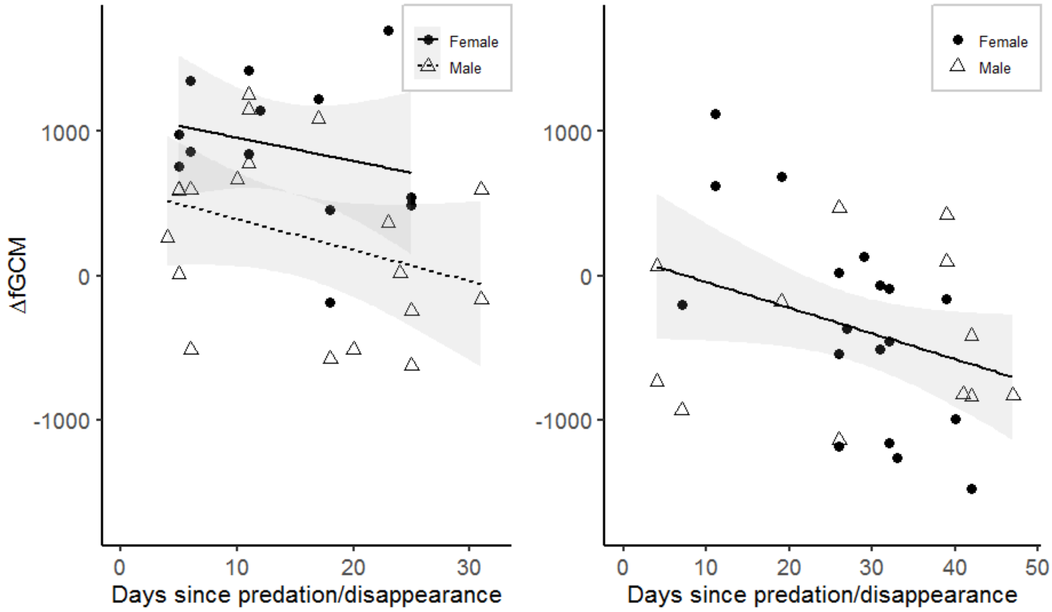


Figure 3.15 Change in fGCM concentrations from (pre-predation) baselines, Δ fGCM, plotted by the number of days since the first predation or disappearance event of period 1 on the left, and period 2 on the right (n = 12 individuals). As shown in the legends, sex is marked by shapes and, for period 1, by line type. Lines represent simple linear regressions between the number of days and Δ fGCM, with shaded areas marking 95%-CIs (period 1: Δ AIC_C = 0 and R^2 = 25.61%; period 2: Δ AIC_C = 0 and R^2 = 17.97%).

Effect of predation or other environmental factors?

Period 1

To investigate whether the findings described above are caused by the predation event or other environmental factors, LMMs were constructed including a ‘before/after predation’ categorical factor as well as weather variables. While the main interest was in the investigation of the increase in fGCM levels in period 1, period 2 was investigated in a similar fashion for comparability reasons. As sex was found to be a significant predictor of the increase in fGCM by time, the following analyses were conducted for males and females separately. Full models were compared with null models which included the same predictors minus the ‘before/after predation’ factor. Results of model comparisons are shown in Table 3.6, while details of the full models are compiled in Appendix III-II.

For males, fGCM values had to be $\log_{10}$-transformed to assure compliance with model assumptions. Here, both the full and null model received substantial support even though the null model had the lower AIC_C. The marginal effect size of the full model was only slightly larger by 3% compared to the null model.

For females, only the full model received substantial support as the null model's $\Delta\ \text{AIC}_\text{C} = 8.82$. Here, the effect size of the full model was about 12% higher than the effect size of the null model. Thus, in line with the results presented above, events that occurred during period 1 appeared to affect females' but not males' fGCM levels.

Male LMM: *log_{10}(fGCM) ~ before/after + maximum temperature + minimum temperature + rain/day + rain/month + age + rank category + (1|individual)*

Female LMM: *fGCM ~ before/after + maximum temperature + minimum temperature + rain/day + rain/month + age + rank category + reproductive state + (1|individual)*

Table 3.6 Results of the LMM comparisons regarding the link between predation and disappearance events of period 1 (included as a categorical factor: before vs after the disappearance/predation) and fGCM concentrations of males and females. Models included maximum and minimum daily temperature, rainfall per day and per month, age, and rank category. For females, reproductive state was also included. ID was used as random factor. Models with a $\Delta\ \text{AIC}_\text{C} < 2$ were considered to have received substantial support and are marked in bold and underlined.

	MALES		FEMALES	
	Response variable: ($\Delta\ \text{AIC}_\text{C}$, marginal R^2 [%])			
	fGCM			
Predictor:	**$\Delta\ \text{AIC}_\text{C}$**	**R^2**	**$\Delta\ \text{AIC}_\text{C}$**	**R^2**
before/after	**1.25**	**27.65**	**0**	**42.55**
null	**0**	**24.92**	8.82	30.14

Period 2

Overall, there was a decrease in fGCM levels from the 'after predation' 1 period through the 'before' and 'after predation' 2 periods. In this subset of data, the monthly rainfall differed significantly between the 'before' and 'after' category of period 2 (ANOVA, $F(1,62) = 208.1$, $p < .0001$), likely reflecting the beginning of the rainy season.

Therefore, for both males and females, two full models were constructed with either the predation factor or monthly rainfall as variables. Additionally, maximum and minimum daily temperature were highly correlated in the male subset (Pearson's product moment correlation, t(62) = 7.28, r = 0.679, p < .0001, CI = 0.52, 0.79). As minimum daily temperature was found before to be a better predictor of fGCM variation in males than maximum daily temperature, it was included in the models here. Results of model comparisons are shown in Table 3.7 and model details are given in Appendix III-II. The progression of fGCM concentrations over both period 1 and 2 as well as the monthly rainfall during those time periods are shown in Figure 3.16.

In this analysis, results for males and females were very similar. In both sexes, both full models received substantial support based on AIC_C comparisons, while the null models had a Δ $AIC_C > 2$. Marginal effect sizes of the full models were comparable. As monthly rainfall significantly increased from the 'before' to the 'after predation' period and fGCM concentrations decreased, it is the more parsimonious explanation that fGCM concentrations decreased in response to increased rainfall, or other associated environmental factors such as potentially increased food availability, and that fGCM levels would not decrease in response to disappearances or predation events.

So overall, the results indicate that fGCM concentrations increased after the first predation and emigration events, with a stronger increase in females than in males. fGCM concentrations subsequently returned to baseline levels in the 'before predation 2' period, and then decreased further despite further predator attacks, which might be linked to increases in monthly rainfall as Figure 3.16 shows.

Male LMM: *fGCM ~ before/after OR rain/month + minimum temperature + rain/day*

+ age + rank category + (1|individual)

Female LMM: *fGCM ~ before/after OR rain/month + maximum temperature*

+ minimum temperature + rain/day + age + rank category

+ reproductive state + (1|individual)

Table 3.7 Results of the LMM comparisons regarding the link between predation and disappearance events of period 2 (included as a categorical factor: before vs after the disappearance/predation) and fGCM concentrations of males and females. Models included either the before/after factor or rain per month as fixed effects. All models included minimum daily temperature, rain per day, age, and rank, and for females additionally maximum daily temperature and reproductive state. ID was used as random factor. Models with a Δ $AIC_C < 2$ were considered to have received substantial support and are marked in bold and underlined.

	MALES		FEMALES	
	Response variable: (Δ AIC_C, marginal R^2 [%])			
	fGCM			
Predictor:	**Δ AIC_C**	**R^2**	**Δ AIC_C**	**R^2**
before/after	**<u>0</u>**	**<u>23.21</u>**	**<u>0</u>**	**<u>25.19</u>**
rain/month	**<u>0.95</u>**	**<u>22.06</u>**	**<u>0.39</u>**	**<u>24.83</u>**
null	2.17	16.72	3.72	21.69

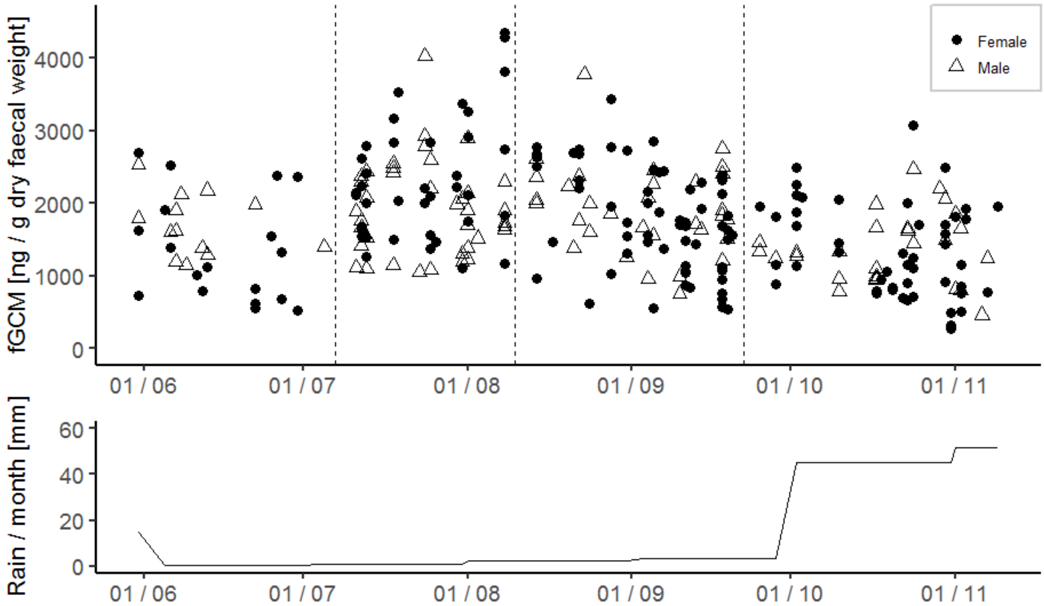


Figure 3.16 Males' and females' fGCM concentrations [ng/g dry faecal weight] over the time period of disappearances and predation events (top graph). The beginning of each new period is marked by a dashed vertical line, i.e. in progression: before predation 1, after predation 1, before predation 2, and after predation 2 periods. Shape marks sex as shown in the legend. Bottom graph shows monthly rainfall [mm] over the same time period.

3.3.3 Summary

In this chapter, mean physiological stress response levels and stress reactivity were investigated in their link to demographic factors in a comparative manner, and changes in fGCM concentrations in response to environmental variables such as weather and predation events were explored (for an overview of results see Table 3.8). Females tended to have higher demonstrated reactive scope values, reflecting higher stress reactivity, than males, while there were no differences in mean fGCM concentrations between the sexes. There was some evidence that mean fGCM concentrations increased during adulthood and then decreased in older individuals, and that demonstrated reactive scope might increase in old age, at least in males. Females had lower fGCM concentrations when they were lactating compared to when they were cycling or pregnant, and high-ranking females had higher mean fGCM concentrations than low-ranking females, while there was only weak support for a potentially similar rank-related difference in males. Generally, males and females experienced increased thermoregulatory demands during times of low temperatures, as represented by higher fGCM concentrations, while fGCM concentrations decreased at the beginning of the rainy season. Regarding the effect of predation, there was evidence that females had increased fGCM concentrations in response to the first predation event recorded in the study troop in several years, while there was no such response in males.

Table 3.8 Summary of the results of chapter 3, investigating inter-individual variation in physiological stress response measures (mean fGCM concentrations, and DRS and DRS$_{CV}$ as measures of demonstrated reactive scope) and their link to demographic factors, as well as the link between environmental factors (i.e. climate and predation) and fGCM concentrations. Findings supporting predictions are marked by a grey background; direction of differences between categorical factors are indicated by < or >, direction of estimates of fixed effects in LMMs are indicated by ↓ for negative prediction and ↑ for positive prediction (♀ = female, ♂ = male, ns = not significant).

Hypothesis 1: Individuals differ in their mean physiological stress response levels and stress reactivity and this variation is linked to demographic factors.			
	Mean fGCM	**DRS**	**DRS$_{CV}$**
Inter-individual differences	sample fGCM: p < .001 monthly means: ns		
Sex	ns	♀ > ♂ (p = .039)	♀ > ♂ (p = .039)
Age	♀: middle-aged > old (p = .024) ♂: young > adolescent (p = .031) young > old (p = .011)	♀: ns ♂: old > middle-aged (p = .011)	♀: ns ♂: ns
Reproductive state	fGCM: lactating < cycling & pregnant (p = .013 and p = .010)		
Dominance rank position	♀: higher rank > lower rank ♂: weak evidence for: higher rank > lower rank	♀: ns ♂: ns	♀: ns ♂: ns

Hypothesis 2: Ecological factors influence physiological stress response levels.		
	Males	**Females**
Climate	min. temp. ↓	max. temp. ↓ reproductive state*min. temp. ↓ for lactating females
Predation	period 1: ns period 2: ns	period 1: increase in fGCM after predation period 2: ns

3.4 Discussion

The aim of this chapter was to compare the links between mean physiological stress response levels and stress reactivity, and demographic factors, as these represent different fitness-relevant aspects of the physiological stress response system, as well as explore the link between environmental factors and fGCM concentrations in this troop of chacma baboons living in a montane habitat. I found evidence that mean physiological stress response levels and stress reactivity linked to demographic factors differently, as for example mean fGCM concentrations differed by rank in females, and potentially males, while demonstrated reactive scope did not. For females, fGCM concentrations also differed with their reproductive state, and there was some evidence that, depending on the reproductive state, the energetic demands linked to thermoregulatory processes might differ. Generally, males and females of the study troop experienced higher energetic demands with lower ambient temperatures, reflecting the challenges of a montane habitat. Additionally, I found evidence that females but not males responded with increased fGCM levels to the predation of a female troop member.

3.4.1 Demographic factors

Hypothesis 1: Individuals differ in their mean physiological stress response levels and stress reactivity and this variation is linked to demographic factors.

Prediction 1i: Individuals differ in their mean fGCM concentrations.

There was some evidence that individuals differed in their mean fGCM levels and in their demonstrated reactive scope, even though the latter could not be analysed statistically due to limited sample sizes. When using sample fGCM concentrations, there seemed to be significant inter-individual differences in these concentrations, while there were no statistically significant differences between individuals when using monthly mean fGCM concentrations. While these results are generally in accordance with a previous study that found inter-individual differences in mean fGCM levels and DRS_{CV} in Barbary macaques (*Macaca sylvanus*; Tkaczynski, 2017), it is striking that there were no inter-individual differences when using monthly means. There are at least two different explanations for this: (i) monthly means mask some of the variation in fGCM concentrations as they reign in outliers, which could make it more difficult to find inter-individual differences compared to using sample fGCM concentrations; (ii) all individuals need to utilise a range of GC concentrations over the study period, e.g. linked to seasonal variation in their environment as well as reflecting increases in GCs in responses to aversive situations, leading to individuals having over-lapping GC ranges. Thus, even though some individuals might have generally higher fGCM levels than others, these might be difficult to statistically detect, especially with relatively small sample sizes. Nevertheless, there was some evidence that individuals might differ in their fGCM levels, and these inter-individual differences provide the basis for an investigation into factors influencing physiological stress response levels and reactivity.

> **Prediction 1ii:** Mean fGCM concentrations and demonstrated reactive scope differ between the sexes.

Studies in rats (Nelson, 2005) and a range of non-human primate species (e.g. mountain gorillas [*Gorilla beringei beringei*; Eckardt et al., 2016]; black capuchins [*Sapajus nigritus*; Moreira et al., 2016]; long-tailed macaques [*Macaca fascicularis*; van Schaik et al., 1991]; Barbary macaques [*Macaca Sylvanus*; Tkaczynski, 2017]) found that sexes differ in their mean and basal physiological stress response levels, in that generally females seem to have higher GC concentrations than males, which could be linked to different body sizes in sexually dimorphic species. This contrasts with the findings of this study as males and females of this baboon population did not differ in mean fGCM concentrations.

Based on the above-mentioned previous work, the general idea would be that males tend to have lower baseline GC concentrations and thus lower mean fGCM levels than females, potentially linked to the larger energetic reserves of larger bodies (Romero and Wingfield, 2015). Here, however, males and females had similar mean fGCM concentrations, which can be explained by two scenarios: (i) in accordance with previous work, males have lower basal GC levels but higher stress reactivity, which could then lead to similar mean fGCM levels of the sexes. However, females of the study troop utilised a larger range of this mediator than males, as described below, meaning that with a higher stress reactivity and higher baseline levels, females would also have higher mean fGCM concentrations. Thus, it seems more plausible that (ii) males have similar if not higher basal levels than females so that they have comparable mean fGCM levels while using a smaller range of GC. This is in accordance with the presented data, as can be seen for example in Figure 3.1 and Figure 3.2, as 12 out of 19 females, i.e. 63%, had monthly means below 1000 ng/g dry faecal weight, while only 3 out of 11 males, i.e. 27%, had monthly means below 1000 ng/g dry faecal weight. This suggests that males of the study troop have higher baseline GC concentrations while showing lower stress reactivity, and thus have similar mean fGCM concentrations to females.

This study also differs in its findings regarding sex differences in demonstrated reactive scope to the previous study of Barbary macaques (*Macaca sylvanus*), which found that males and females did not differ in their DRS_{CV} (DRS was not tested) (Tkaczynski, 2017). The current study provides the first evidence for a difference in DRS and DRS_{CV} between the sexes; the DRS and DRS_{CV} of females were higher than of males and females also showed a wider absolute range of measurements, indicating that females of the study troop had higher stress reactivity or experienced more variation in energetic demands during the study period than males.

While these results differ from the above cited study on Barbary macaques, and studies on HPA-axis reactivity in non-human primate species are very limited, sex differences in stress reactivity have been studied in rodents for decades, with generally congruent results to the ones presented here (Kudielka and Kirschbaum, 2005): in rats, early studies found that females showed stronger HPA-axis reactivity measured as higher increases in corticosterone levels in response to laboratory stressors (Haleem et al., 1988) and that the activation also lasted longer in females than in males (Heinsbroek et al., 1991). As Panagiotakopoulos and Neigh (2014) review in detail, sex-specific physiological differences can affect the development of various parts of the HPA-axis at different stages, and sex-specific differences in hormonal concentrations, such as concentrations of androgens and oestrogens, can influence HPA-axis reactivity during adulthood as well. Broadly speaking, testosterone seems to be one of the major factors leading to a dampening the HPA-axis response (Panagiotakopoulos and Neigh, 2014), which provides one potential explanation of why males of the study troop tended to have lower demonstrated reactive scope than females.

It should also be considered, though, that, as described in the introduction of this chapter, males and females experience very different energetical demands and social stressors, for example linked to their reproductive system or their social relationships. Therefore, besides differences in their physiology and body size, experiencing different types and quantities of stressors might also be the reason that the range of GC they needed to utilise to cope with these demands differed, leading to the sexes differing in their demonstrated reactive scope.

> **Prediction 1iii:** Mean fGCM concentrations and demonstrated reactive scope differ between age classes.

Results of this study suggest that GC levels differ between age classes. While most studies find either no link between age and fGCM concentrations (e.g. Bergman et al., 2005) or an increase in GC levels with higher age (Alberts et al., 2014), young male adults in the study population had higher mean fGCM concentrations than both adolescent and old males. The increase of physiological stress response levels from adolescence to young adulthood is in agreement with previous findings (olive baboons

(*Papio anubis*) and hamadryas baboons (*Papio hamadryas*); Fourie et al., 2015) and probably represents a developmental change. The differences between the various adult stages, however, is surprising. It is unclear whether the hypercortisolism of older age found in some studies only occurs after a specific age, and whether the old males of this study might not have reached that age yet. Alternatively, the results could reflect something specific to the study population, where old males might experience for some reason lower environmental or social stress than in other populations. It should be noted, however, that there are only two males included in the middle- and old-age category each. This obviously makes the results less reliable, even though the congruence between each of the two males, especially in the middle-age category, is striking. Additionally, it should be noted that age does not come out as a significant predictor of fGCM levels in any of the later analyses.

For females, adolescent individuals were not included in this study, thus no conclusion can be made about potential changes through developmental stages until adulthood in females. There are, however, similar patterns to the ones in males, in that fGCM levels increase and, here, peak in middle-aged females with a subsequent, significant decrease in old females. However, the results of other models indicated that the effect of age might not be as strong as those of other demographic factors. So, while mean fGCM levels of the age classes differ, age might not have as much explanatory power as other factors influencing fGCM concentrations.

Regarding demonstrated reactive scope, no previous study has explored age effects on DRS or DRS_{CV}. For males, it is remarkable that old males, who had the lowest mean fGCM values, had significantly higher DRS and DRS_{CV} values than middle-aged individuals. So, while mean levels of fGCM could be described by a downward U-shape, demonstrated reactive scope seems more variable between the age classes, with a significant increase in old males. Interestingly, there was no significant difference for either DRS or DRS_{CV} between age classes for females.

These results suggest that age has a different effect on mean physiological stress response levels and stress reactivity in male and female chacma baboons. Additionally, for females there might be other factors, such as rank, that might be better at explaining variation in fGCM levels and demonstrated reactive scope than age.

Prediction 1iv: Female fGCM concentrations vary with reproductive state.

There are many ways in which reproductive state can influence fGCM levels in females. For example, GC levels have been shown to increase during pregnancy due to physiological changes (Mastorakos and Ilias, 2003). Depending on the species, lactation can also be linked to increased GC concentrations, potentially due to the risk of infanticide (Weingrill et al., 2004), but also to decreased levels of GC, potentially in cases of low threat of infanticide and due to the stress-mitigating effect of increased oxytocin concentrations caused by suckling (Uvnäs-Moberg, 1998).

In accordance with some previous findings, reproductive state did influence fGCM levels in this study. However, while other studies of chacma baboons found increased levels of GCs during pregnancy (Weingrill et al., 2004; Beehner et al., 2005; Engh et al., 2006b), here fGCM levels of pregnant females did not differ from those of cycling females in the longer term. Lactating females, however, had lower fGCM concentrations than both cycling and pregnant females, which is likely linked to the low levels of infanticide threat and the potentially stress-mitigating effects of raised oxytocin concentrations due to suckling. Fittingly, no infanticide has been observed yet in this population of chacma baboons. Overall it should be noted that sample sizes are relatively low due to the long gestation period relative to data collection time, and low numbers of faecal samples from some females. Therefore, while these results give some first indication of potentially lowered physiological stress response levels during lactation, the results should be interpreted with caution. Nevertheless, reproductive state will be incorporated as control factor in further analyses of sample fGCM levels where appropriate. Due to the small sample sizes, no analysis into whether females of different reproductive states differed in their demonstrated reactive scope was possible.

Prediction 1v: Mean fGCM concentrations and demonstrated reactive scope are linked to dominance hierarchy position.

Dominance rank position is assumed to be an important factor influencing the social life of baboons and their lifetime reproductive fitness, due to differential access to food, matings, or social support depending on the position in the hierarchy (Majolo et al., 2012). Similarly, hierarchy stability has been described to have important implications for the physiological stress response levels of dominant and subordinate individuals (male chacma baboons - Bergman et al., 2005; female chacma baboons - Engh et al., 2006b). In this study, no phases of clear stability or instability could be discerned as described in chapter 2; however, mean physiological stress response levels did vary between rank categories in a sex-specific way.

For males, aggression tends to be one of the main mechanisms of rank acquisition and maintenance, which means that in most species, males experience different social stressors and thus have different physiological stress response levels depending on their rank (e.g. Kalbitzer et al., 2015). However, there was only weak evidence that higher ranking males might have higher mean physiological stress response levels than low-ranking males, and no link between demonstrated reactive scope and dominance rank position in males. While this finding contrasts with previous research, it does fit with the observation that male rank determination for this study took a long time, as shown in the graphical representation of the development of Elo-ratings over time in chapter 2. Additionally, access to receptive females and securing of consortships is normally assumed to be one of the main advantages of high rank for males (Alberts et al., 2006). In this study population, however, almost all adult males did manage to procure a consortship and are assumed to have fathered offspring during the last couple of years. Whether this absence of a strong correlation of rank and physiological stress response measures is indeed due to a less stringent hierarchy or generally low levels of aggression, needs to be investigated further. It does, though, bear resemblance to the 'pacific culture' that evolved in a troop of olive baboons (*Papio anubis*) once the most aggressive males had died (Sapolsky and Share, 2004), so a comparison of aggression rates between different populations would be a useful next step. Apart from this, the only weak link between high dominance rank position and higher mean fGCM concentrations of males might be a specific feature of this population, for example due to specifics of the habitat or due to the makeup or formation of the troop.

In contrast to males, females' mean physiological stress response levels, but not their demonstrated reactive scope, did clearly differ by dominance rank position. While most studies of female chacma baboons found either no correlation of rank and GCs (e.g. Beehner et al., 2005) or higher GC levels in subordinate individuals (reviewed in Cavigelli and Caruso, 2015), in the study population high-ranking females showed higher mean fGCM levels than lower ranking females. This is in accordance with studies on female Barbary macaques (*Macaca sylvanus*; Gustison et al., 2012) and ring-tailed lemurs (*Lemur catta*; Cavigelli and Caruso, 2015). While the observed relationship held both when using mean randomised Elo-ratings or rank categories, the results of the latter analysis are more striking, as females of category 1 and 2 seem to have mostly higher mean fGCM concentrations than females of category 3 and 4. In chacma baboons it is normally assumed that females inherit their rank from their mothers and very rarely use aggression to attain higher ranks (Cheney, 1977), which would explain why mean fGCM levels would not vary by rank, and that low-ranking females, if any, experience higher levels of social or nutritional stress (Seyfarth et al., 2012; Cavigelli and Caruso, 2015), which explains why low-ranking females often show higher levels of physiological stress than higher ranking females. Therefore, it will need further investigation to interpret the positive correlation found here.

In general, female chacma baboons' dominance hierarchies are structured along matrilines (Silk et al., 1999), so that differences in physiological stress response levels between dominance rank categories could potentially also reflect genetic predispositions to higher or lower GC levels (e.g. due to differences in genetically determined receptor densities). However, as described in chapter 2, section 2.2.1.2, no data on kinship were available and no matrilines were discernible based on patterns of affiliation or physiognomy.

As is the case for males, the unexpected rank-differences in mean fGCM levels found here might reflect something specific about the study troop or the habitat they live in, that distinguishes the study population from previously studied populations of chacma baboons in other habitats. For example, while it is generally assumed that high rank comes with benefits such as priority access to food sources (Majolo et al., 2012), it is possible that the widely spread food sources found in the study troop's home range negate any disadvantages normally associated with lower rank, or that the wide spatial spread of the troop (linked to the widely spread food sources) means that low-ranking females can avoid most aggression normally directed towards them by higher ranking females, and thus do not experience more social or nutritional stressors than higher ranking females. Another possibility is that high-ranking females have to cope with more social stressors, e.g. by receiving aggression by males at higher rates than lower ranking females might. Considering that no clear matrilines were discernible in this troop, as described above (suggesting that it might have undergone some drastic event that changed the group composition), it is also a possibility that high-ranking females do have to maintain their rank by aggressive encounters, which might be more stressful for higher-ranking individuals. A study of female ring-tailed lemurs (*Lemur catta*), a naturally matriarchal society, also found that high-ranking females had higher mean fGCM levels, and that those were due to higher maximum fGCM levels but not increased minimum measures (Cavigelli and Caruso, 2015), which suggests a higher stress reactivity rather than chronic elevation. While there were no rank-related differences in demonstrated reactive scope in this baboon population, it would be a useful next step to compare minimum and maximum fGCM concentrations between rank categories to discern in more detail whether the higher mean levels are due to a general increase or, as in the lemurs, due to higher stress reactivity.

3.4.2 Environmental factors

Hypothesis 2: Ecological factors influence physiological stress response levels.

Prediction 2i: fGCM concentrations are influenced by climatic variation.

There are many ways in which climatic factors might influence individuals' physiological stress response levels as described in the introduction of this chapter. Here, I found that temperature, but not rainfall, was linked to fGCM variation in a sex-specific way. While in both sexes, individuals had higher fGCM concentrations when ambient temperatures were low, males' fGCM concentrations were best predicted by minimum daily temperatures, whereas females' fGCM levels were best explained by maximum daily temperatures. Additionally, minimum daily temperature was linked to females' fGCM levels depending on their reproductive state, in that lactating females had higher fGCM concentrations when minimum temperatures were low, while cycling and pregnant females did not.

Only one study so far has investigated specifically the link between weather factors and physiological stress response levels in male baboons in southern Africa. A study on yellow baboons (*Papio cynocephalus*) in Kenya found that males had higher fGCM levels during the dry compared to the wet season, but found no direct link between fGCM levels and temperature measures (Gesquiere et al., 2011b). While seasonality was not quantified in the context of the current study, visual inspection of the temperature and rainfall graph in chapter 2 seems to indicate that lower temperatures might coincide with the period of least rainfall. Thus, it is possible that the link between temperature and fGCM levels found here might reflect the finding of fGCM variation with season described by Gesquiere et al. (2011b), but in this current study there was a strong link of minimum daily temperature to fGCM levels which was not observed in the yellow baboons.

For females, the results presented here are consistent with earlier findings that female chacma baboons in a savanna habitat showed higher GC levels with less daylight, i.e. in winter (Weingrill et al., 2004). While I did not use daylight hours as a parameter, maximum temperatures tended to be lower in the months of May to September, i.e. in winter, and were linked to higher fGCM levels in females. In yellow baboons (*Papio cynocephalus*) in Kenya, on the other hand, high GC levels were linked to higher maximal daily temperatures (Gesquiere et al., 2008), which is in direct contrast to my findings, and potentially reflects different thermoregulatory demands connected to the different habitats.

Additionally, the link of temperature to fGCM levels seemed to be influenced by reproductive state in the females of this study. While other studies incorporated these factors into their models (e.g. Gesquiere et al., 2008), this is to my knowledge the first support for a differential effect of weather on physiological stress response levels depending on the female's reproductive state. Here, I found that minimum daily temperature, while only having a marginal effect on fGCM levels on its own, becomes a significant predictor in combination with reproductive state; the direction of correlation between minimum temperature and fGCM concentrations differs between lactating and non-lactating females, where lactating females have higher fGCM concentrations with lower minimum temperatures, while cycling and pregnant females had higher fGCM concentrations when minimum temperatures were higher. While further investigations into these links are needed, this hints at females in different reproductive states experiencing, for example, different social or ecological stressors, potentially based on their energetic needs, or expressing different rates of behaviours that might be linked to GC concentrations.

There are two main potential reasons why the results of this study mostly do not match with the studies mentioned above. Firstly, both studies by Gesquiere and colleagues were conducted on yellow baboons (*Papio cynocephalus*; Gesquiere et al., 2008; Gesquiere et al., 2011b). While this is a closely related species, differences in geographical range and thus differences in habitat as well as differences in evolutionary constraints might mean that species differ in the environmental challenges they experience as well as how they evolved to deal with these challenges. Additionally, both the studies on yellow baboons and the study on chacma baboons by Weingrill et al. (2004) were conducted in savanna habitats. Challenges and constraints might vary considerably between savanna and montane habitats. For example, maximum and minimum temperatures might differ considerably between habitats so that baboons experience either heat or cold as a stressor. Furthermore, they might experience temperature and thus use thermoregulatory processes differently depending on the amount of shade and wind chill, for example. Additionally, food scarcity and its link to weather variables might differ, as well as how rainfall and temperature correlate with each other. Finally, predation pressure and thus vigilance behaviour might be weather dependent – dense fog in the mountain often occurs when there is high humidity but no rain, which might influence the baboons' vigilance behaviour or travelling routes and in turn GC concentrations.

Overall, this study provides evidence for a link of physiological stress response levels to weather conditions in this baboon population, specifically a negative correlation between temperature and fGCM concentrations. Additionally, this link seems to slightly differ between males and females, and, for the latter, reproductive state appears to influence how weather affects GC levels.

Prediction 2ii: fGCM concentrations increase after a predation event.

As described in the introduction of this chapter, predation is assumed to be one of the major stressors for baboons in the wild. While this study does not provide the ideal framework for an investigation into the consequences of predation on the remaining troop members, due to the low number of confirmed predation events and overlapping ‘time frames’ between these events, it does yield some interesting results. fGCM levels increased significantly in the month after the first predation event, but not the second, and the increase was strongest shortly after the first predation. These findings are in line with the study by Engh et al. (2006a), who found significantly increased fGCM concentrations in the four weeks after predation, compared to levels before this event.

While Engh and colleagues only included females, this study investigated the effect of predation on physiological stress response levels in both males and females. Sex turned out to be a significant predictor of the increase of fGCM levels after predation one, in that females’ fGCM concentrations increased while males’ did not, so that all further analyses were conducted separately for males and females.

Previous analysis had shown an effect of weather on fGCM levels in this troop and other studies have described monthly variation in mean fGCM levels in baboons (e.g. MacLarnon et al., 2015), so that this peak after predation could also potentially coincide with seasonally heightened hormone levels. However, in models including both environmental data and a factor on whether the faecal sample was collected before or after the predation event, the model including the latter factor was substantially better when analysing females’, but not males’, fGCM data. Considering that in baboons females are the philopatric sex while males disperse, it makes sense that the loss of an adult female baboon would be inherently more stressful for females than for males, as this female was peer and relative for at least some of the females.

Engh et al. (2006a) found that females who lost a relative had increased fGCM levels after the attack while females who did not lose a relative did not show increased levels. Unfortunately, sample sizes in this study were too small and no kinship data were available, so that an analysis in this regard was not possible. However, during observations of the study troop, no signs of matrilines or kinships were clearly discernible, as discussed before. Thus, social non-kin bonds might play a more important role in the troop, but due to the small sample size it is not possible to investigate differential physiological stress responses based on social bond strength systematically. In chapter 4, though, behavioural responses to the predator attacks will be investigated and the dyadic bond strength to the killed individual will be included there.

Interestingly, fGCM levels only further decreased from thereon until the end of the study period despite several disappearances and another confirmed predation event. During this time period, though, rainfall increased substantially and at the same time as the first disappearances. Thus, this change in weather might have had a stronger influence on the individuals' fGCM levels than the predation and disappearances and might have caused the observed decrease in fGCM concentrations. Additionally, period 2 differed from period 1 in some important ways: firstly, the predation in period 1 was the first recorded leopard attack on an adult troop member in several years and might have therefore inherently been more stressful to the whole troop due to the unexpectedness. Afterwards, the baboons might have adapted their vigilance or habitat use to the presence of this new leopard, which had just set up its territory in the baboons' home range. Secondly, while several disappearances and one confirmed predation event happened in period 2, the females that disappeared were low-ranking and/or old females and the individual that was killed was a low-ranking male, while the killed individual in period 1 was a relatively high-ranking, infant-carrying female. Thus, the identity of the lost individual might play an important role in the severity of the response of the rest of the troop. This is in accordance with a study in chacma baboons utilising a social network approach, that showed that the loss of a high-ranking individual affects the behaviour of all troop members similarly, while the loss of a low-ranking individual does not (Barrett et al., 2012).

Overall, even though sample sizes are small and there might be overlapping and/or contradicting effects of weather and predation on the individuals' fGCM levels, it seems plausible that the first but not the second predation event led to increased physiological stress response levels of the female baboons. The differing effect of predation depending on the identity of the killed individual, or the circumstances of death, as well as the difference in response between the sexes, is striking and will require further investigation with a larger dataset. Even so, the difference in response between the sexes hints at a differential importance of social relationships and networks for males and females in a baboon troop and therefore means that the loss of a troop member might impact individuals differently, based on their sex, kinship, and potentially their bond to the killed individual.

3.4.3 Conclusion

This chapter presents a first investigation into stress reactivity, measured as demonstrated reactive scope, in a baboon population and described a comparative analysis of how mean physiological stress response levels and demonstrated reactive scope linked to demographic factors. While demonstrated reactive scope was linked to sex and age, i.e. females had higher demonstrated reactive scope than males and demonstrated reactive scope increased with older age in males, mean physiological stress response levels were also linked to age but were additionally linked to dominance rank position and reproductive state. Here, mean fGCM concentrations increased in middle-aged individuals and decreased again in older animals, fGCM levels were higher in high-ranking than in low-ranking individuals, and they were lower in lactating than non-lactating females. Additionally, weather variables were found to influence fGCM concentrations differently for males and females, and there was some evidence that the effect might depend for females on their reproductive state, but overall baboons of the study troop seemed to experience thermoregulatory demands connected to low temperatures. This study is one of the few to describe the effect predation has on the physiological stress response levels of the remaining troop members. While males did not show a change in fGCM levels in response to the attack, females' fGCM concentrations increased significantly after a leopard attack. This response, however, did seem to be dependent on the identity of the killed individual or the circumstances of the death. Overall, this chapter provides insights into mean physiological stress response levels and stress reactivity of this montane baboon population and hereby provides the basis for further investigation into stress-related behaviour and resilience in this troop in the following chapters.

4. Coping behaviour and social buffering in chacma baboons

4.1 Introduction

In the natural world, animals experience many different kinds of abiotic and biotic, labile and permanent perturbations, which can threaten homeostasis, their food availability, or their home range integrity (Romero and Wingfield, 2015). Examples of biotic perturbations include food scarcity, parasites, predators, disease or threatening social interactions, whereas abiotic perturbations might be weather phenomena, extreme temperatures, fires or storms. There might also be longer term perturbations, for example through climate change, pollution, or human disturbance. These can lead to the same changes in the environment as the labile perturbations, but require adaption of the species or might lead to local extinction (Romero and Wingfield, 2015). Animals have to deal with perturbations on a daily basis, as a normal part of the natural environment, and the baboons of the study troop experienced perturbations from all these categories: heat and cold during different times of the year, food shortage because of a drought, severe thunderstorms, predation, disease and parasites, as well as human disturbance in the form of farming activity in their home range.

4.1.1 Coping

The term coping generally means dealing with something challenging in an effective way (Lexico, 2019). In the context of the natural perturbations described above, coping will often be mediated by activation of the HPA-axis. Here, the general stress response, as described in detail in chapter 1, will be mounted in response to a stressor and, as such, help individuals cope with labile perturbations. For example, when attacked by a predator or conspecific, the general stress response can help mobilise the energy needed to fight or escape, and if an injury is sustained, GCs play a vital role both in the mobilisation of immune cells and in providing negative feedback to prevent an overactive immune response (Romero and Wingfield, 2015). As chronically elevated levels of GCs can have detrimental effects, however, a quick and efficient termination of the stress response is also important to avoid negative consequences such as immune suppression or reduction of fertility (Nelson, 2005).

In the context of this study, the main interest lies in the inter-individual differences in animals' ability to cope with these everyday stressors. While a large part of an animal's capability is potentially determined by genetics and epigenetics, pre- and post-natal experiences, as well as life-history stage (Koolhaas et al., 1999), there might also be behavioural strategies animals can utilise to influence their stress response. Such behavioural responses to a stressor have been termed coping behaviour (Lazarus, 1966). As described in chapter 1, coping behaviour has been defined as a behavioural response to an aversive situation, with the aim of removing the aversive stimulus or reducing the physiological effects caused by the stressor (Wechsler, 1995), and as such attenuating the effect of the stressor on fitness or fitness-related physiological measures. Coping behaviour, however, might not always be successful and should therefore not be defined by its success in removing the stressor (Wechsler, 1995). Furthermore, studies have shown that coping behaviour might affect behavioural and physiological consequences of stress differently, so that 'success' might not necessarily be behaviourally measurable (Helmreich et al., 2012).

4.1.2 Potential coping behaviours in primates

While Wechsler (1995) suggested classifying coping behaviours into four coping strategies for inter-species comparability (i.e. distancing themselves from the stimulus, removing the stimulus, search and appetitive behaviour, and waiting or apathetic behaviour), as has been described in chapter 1, three main potential coping behaviours of primates have been suggested in response to stressors: individuals could react aggressively towards the aversive stimulus or a third-party, they could use affiliative behaviour such as grooming to potentially mitigate the negative physiological consequences of the general stress response, or they could show self-directed behaviour (Gustison et al., 2012). These three categories of behaviour and their study in non-human primate species will be described in the following.

4.1.2.1 Aggression

Aggression towards the stressor is an obvious choice of behavioural reaction during many stressful situations, such as predator attacks or social conflict (Wittig and Boesch, 2003). In addition, redirection of aggression towards non-involved bystanders has been described in several baboon and macaque species (reviewed in Cheney and Seyfarth, 2009; olive baboons [*Papio anubis*; Virgin and Sapolsky, 1997]; macaques, Thierry, 1985; Paschek et al., 2019), which might also be interpreted as coping behaviour, especially if the initial conflict partner is still a threat. A study in female Barbary macaques (*Macaca sylvanus*), for example, found that individuals showed increased rates of aggression in the 20 minutes following a mild, experimentally induced stressor (Gustison et al., 2012). Regarding its link to GCs, the same study found that median fGCM concentrations were positively linked to changes in lunge rates but no other aggressive behaviours (Gustison et al., 2012). By contrast, low-ranking male olive baboons that showed more redirected aggression tended to have lower baseline plasma GC concentrations (Virgin and Sapolsky, 1997). In humans, artificially increased GC concentrations led to increased rates of aggressive behaviour among women, but not men, after provocation (Böhnke et al., 2010). These studies suggest that aggression might function as a coping behaviour and might be linked to, or mediated by, GCs and that the effects seem to be species- and sex-dependent.

4.1.2.2 Affiliative behaviour

Describing effects of affiliative behaviour, especially grooming, in the context of coping strategies is potentially difficult, considering the many possible links of affiliation to stress, anxiety, and fitness. Therefore, grooming will first be discussed in its link to anxiety-related behaviours and then in its relation to GC measures. The more general link of social bonds, sociability or social support, often mediated by grooming relationships, to GCs and fitness measures will be discussed subsequently in section 4.1.3. It should be noted that it is difficult to differentiate between effects of affiliative behaviours themselves and effects of more general social buffering on the stress response and that these concepts or interpretations are not mutually exclusive but in fact corroborative. If either the proximity of a bonded partner or an affiliative interaction with this partner can dampen the physiological stress response (potentially mediated by oxytocin, Uvnäs-Moberg, 1998), then these behaviours should also be regarded as potential coping behaviour if an animal seeks out these interactions in stressful situations.

Regarding the link of grooming to anxiety-related behaviours, most studies investigating these links have used scratching and/or other self-directed behaviours as a measure of anxiety, based on early pharmacological studies that showed a decrease of scratching rates after an injection with anxiolytic medication (e.g. Schino et al., 1991, reviewed in Maestripieri et al., 1992), and on studies that found increases in these behaviours in situations that were assumed to be stressful or anxiety-inducing (e.g. Gustison et al., 2012; Paschek et al., 2019). A recent study, however, has suggested that scratching might be linked to positive or negative arousal in a more complex manner (Neal and Caine, 2016), so studies using scratching as a proxy for anxiety or stress should be considered cautiously. Studies conducted in non-human primate species investigating the link between grooming and self-directed behaviours have produced mixed results. In some species it has been found that individuals exhibit lower rates of self-directed behaviour during and after grooming interactions (long-tailed macaques [*Macaca fascicularis*; Schino et al., 1988]; female black crested macaques [*Macaca nigra*; Aureli and Yates, 2010]; female Japanese macaques [*Macaca fuscata*; Schino and Alessandrini, 2015]) and that the individual giving grooming generally showed less aggressive behaviour after grooming (black crested macaques - Aureli and Yates, 2010), suggesting that grooming effectively alleviates anxiety. Studies in Barbary macaques (*Macaca sylvanus*), however, found the opposite link, with scratching rates being higher in both donor and recipient after a grooming interaction compared to matched control periods or mean levels (Molesti and Majolo, 2013; Semple et al., 2013), suggesting that grooming might not always be anxiety reducing, and that the termination of a grooming interaction might indeed be anxiety-inducing.

In addition to studies exploring the link between grooming and self-directed behaviour, others have investigated the relation between grooming and physiological stress response levels measured as GC concentrations. Here, the general finding is that there are negative links between grooming and GC concentrations, such that high levels of grooming predict low concentrations of GCs, but these relations often seem to be rank- and sex-specific. In one study of high-ranking male olive baboons (*Papio anubis*), for example, individuals that showed a lot of socio-positive behaviour including grooming either towards the female they were consorting with, or towards non-oestrous females outside the consortship context, had lower plasma GC baseline concentrations and reactivity (Ray and Sapolsky, 1992), while in a study including both high- and low-ranking male olive baboons, no link between grooming given or received and fGCM concentrations were observed (Ellis et al., 2011). In female chacma baboons (*Papio ursinus*), individuals had, independent of rank or reproductive status, lower fGCM concentrations when their grooming networks were more focused, that is when they concentrated their efforts towards a few grooming partners (Crockford et al., 2008; Wittig et al., 2008). In female Barbary macaques (*Macaca sylvanus*), the results have been varied: Shutt et al. (2007) found that females had generally lower fGCM concentrations the more grooming they showed, measured as grooming duration and clique size. Sonnweber et al. (2015), however, found this effect again to be rank-dependent, in that high-ranking females had lower uGCM concentrations when they focused their grooming on fewer individuals, whereas low-ranking females had lower uGCM levels when they distributed their grooming behaviour more evenly. As mentioned above, differentiating the stress-reducing effect of grooming from effects of social buffering or social support mediated by grooming relationships is difficult, but also not necessarily needed to investigate grooming as coping behaviour in this context.

4.1.2.3 Self-directed behaviour

Self-directed behaviours, such as scratching, auto-grooming, yawning or body-shaking, are very common parts of the behavioural repertoire of non-human primates. They are, however, also shown in situations where they appear irrelevant to the ongoing context and are interpreted here as reflecting the emotional ambiguity or frustration of a conflicting situation (Baker and Aureli, 1997). In these instances, they have been termed displacement behaviours and are often used as a measure of anxiety or arousal. Scratching rates have been shown to increase in typical anxiety-inducing, i.e. potentially stressful, situations such as being in the proximity of dominant individuals (e.g. in female olive baboons [*Papio anubis*; Castles et al., 1999]; Barbary macaques [*Macaca sylvanus*; Paschek et al., 2019]), and overall rates of auto-grooming have been shown to be positively correlated with mean fGCM concentrations in Barbary macaques (Edwards et al., 2013). In a rare experimental study of coping behaviour in free-ranging primates, Gustison et al. (2012) showed that female Barbary macaques increase their scratching rates in the 5 minutes after being exposed to a mildly stressful stimulus.

Contrary to these findings, though, male marmosets (*Callithrix penicillata*) reduced their self-directed behaviour when first exposed to a predator trial compared to the habituation phase, and only significantly increased their rates in the later exposure trials (Barros et al., 2004). Similarly, Neal and Caine (2016) found that common marmosets (*Callithrix jacchus*) increased scratching during play, a situation of positive arousal, but not during standard test situations that are assumed to be anxiety-inducing, in contrast to previous studies. Furthermore, Higham et al. (2009) found in female olive baboons (*Papio anubis*) no correlation between self-directed behaviour rates and fGCM concentrations, either in temporarily matched or averaged data, and similarly, Ellis et al. (2011) found no link between median fGCM concentrations and rates of self-directed behaviour in male olive baboons. Considering that many studies did show increased rates of scratching in potentially stressful situations, self-directed behaviour should be considered as potential coping behaviour following the definition provided above, independent of whether such behaviour is linked to GC concentrations: as Higham et al. (2009) point out, a lack of correlation between these measures could also be the result of self-directed behaviour being a successful coping strategy. Accordingly, Watson et al. (1999), for example, found in male small-eared bushbabies (*Otolemur garnettii*) that individuals that showed high rates of scent-marking as a displacement behaviour had lower plasma GC baseline and response levels to restraint stress, compared to individuals that showed lower rates of scent-marking. Similarly, a study reported that women who exhibited higher rates of displacement behaviour had lower heart rate during a stressful test situation (Pico-Alfonso et al., 2007), while another study reported a similar negative link between displacement behaviour and heart rate in men (Mohiyeddini et al., 2013). Both scratching and other self-directed behaviours will be investigated as potential coping behaviours in this study.

4.1.3 Social buffering

Besides behavioural coping strategies, social bonds have been shown to help animals cope with stress and reduce its effects on their fitness and should as such be considered in the context of coping. As described in chapter 1, the term ‘social buffering’ describes the finding that individuals show a better recovery after a stress response if conspecifics are present (Kikusui et al., 2006) and that their presence can even mitigate the activation of the HPA-axis in response to stressors, as was shown in squirrel monkeys (Levine, 2000).

In accordance with these findings, sociability has been linked to GC measures in a variety of non-human primate species. Besides the previously described studies showing that grooming behaviour specifically is often linked to GC concentrations, social bonds more generally have been linked to GC measures in a few species, as shortly described in chapter 1. For example, in Assamese macaques (*Macaca assamensis*), male-female bonds were linked to lower levels of fGCM in the mating season, whereas, in the non-mating season, females had lower fGCM concentrations when they were bonded more strongly to other females (Fürtbauer et al., 2014). Similarly, male Barbary macaques (*Macaca sylvanus*) were found to have attenuated responses to stressors if they had strong social bonds with other adult males (Young et al., 2014), and female chacma baboons (*Papio ursinus*) experienced an attenuated increase in fGCM during times of instability in the male hierarchy if they had a low grooming diversity beforehand, i.e. if they had been focusing their grooming on a few partners (Wittig et al., 2008). Using a social network approach, Brent et al. (2011) also found that in high-ranking female rhesus macaques (*Macaca mulatta*) more focused proximity networks were associated with lower fGCM concentrations.

Many studies on non-human primate species have used the CSI as a measure of bond strength (see section 2.2.2.2; Silk et al., 2003; Silk et al., 2006b; Silk et al., 2006a) and have linked it to fitness-relevant measures. In females, strong and consistent social bonds have been connected to enhanced infant survival in yellow baboons (*Papio cynocephalus*; Silk et al., 2003) and chacma baboons (*Papio ursinus*; Silk et al., 2009), higher birth-rates in chacma baboons (McFarland et al., 2017), and longer lifespan in yellow baboons (Silk et al., 2010b; Archie et al., 2014) and blue monkeys (*Cercopithecus mitis stuhlmanni*; Thompson and Cords, 2018). Furthermore, number of affiliative partners predicted the survival of both male and female Barbary macaques (*Macaca sylvanus*) during a harsh winter (McFarland and Majolo, 2013). Strong social bonds were additionally linked to increased future cooperation in male Barbary macaques (Berghänel et al., 2011) and to increased reproductive success in male Assamese macaques (*Macaca assamensis*; Schülke et al., 2010).

Besides these effects of strong social bonds, social integration more generally has been suggested to have beneficial effects on individuals' fitness (see also section 2.2.2.2); for example, the number of weak, but not the number of strong, bonds in female chacma baboons was linked to the 12 months-survival of their infants (McFarland et al., 2017). Similarly, Cheney et al. (2016) found in chacma baboons that high Eigenvector centrality in a network (based on dyadic CSIs) was an even better predictor of high infant survival than the actual CSI scores themselves. Similarly, it was shown in Barbary macaques (*Macaca sylvanus*) that an individual's position in an aggression network, i.e. high degree and low clustering coefficient, was a better predictor of survival through an exceptionally cold winter than was bond strength (Lehmann et al., 2015) as was previously identified as important in this respect by McFarland and Majolo (2013).

As described above, there are many factors that determine an animal's stress reactivity, such as genetics, epigenetics, and pre- and post-natal experiences. To a certain degree, however, animals seem to be able to utilise behavioural strategies and mechanisms to mediate their response to stressors. To what extent these behaviours are determined in turn by the inherent and developmental factors mentioned above remains unclear. In general, non-human primates seem to potentially use coping behaviours to respond to aversive situations and form social bonds and social networks that might have beneficial effects on their fitness.

This chapter investigates these potential coping mechanisms in a comprehensive manner: coping behaviour will be investigated as short-term changes in behaviour in response to potentially stressful situations and explored in relation to changes in fGCM concentrations, as well as to variation in longer term physiological stress response measures such as mean fGCM concentrations and demonstrated reactive scope. Then, the link will be explored between long-term rates of behaviour, thought to represent potential cumulative effects of short-term coping behaviour, and both mean fGCM levels as well as demonstrated reactive scope. Both approaches will use the three domains of behaviour that have been suggested to be potential coping behaviours in non-human primates, i.e. self-directed behaviour, affiliation, and agonism. Unfortunately, due to the very difficult terrain and data collection, not enough fGCM data were available to investigate whether behavioural rates were correlated with fGCM concentrations over time, which might have enabled a clearer picture of the temporal link between coping behaviours and physiological stress response measures. Finally, to investigate physiological correlates of strong social bonds and social integration, I will explore the link between social bond strength and network position on the one hand, and individuals' mean fGCM levels and demonstrated reactive scope on the other. To allow a clear distinction between these three approaches, the behavioural responses to specific aversive situations will subsequently be termed 'coping behaviours', whereas overall rates of behaviour, explored regarding their link to mean fGCM concentrations and demonstrated reactive scope, will be called 'long-term coping behaviour', and the link between social bonds or integration and mean fGCM levels or demonstrated reactive scope will be termed 'social buffering'.

4.1.4 Hypotheses and predictions

The above described analyses will be conducted to test the following hypotheses and predictions. Investigating how potential coping behaviours link to physiological stress response measures is complicated, as individuals experiencing higher physiological stress response levels might show increased rates of coping behaviour, while coping behaviour – if successful – could mediate the physiological stress response and thus be linked to lower or not significantly changed physiological stress response measures. Similarly, predicting the link between position in a social network and physiological stress response measures is not unambiguous; here, both affiliative and agonistic network positions were assumed to reflect aspects of the individuals' general social positioning, with centrality in both cases potentially reflecting overall well-connected individuals. Thus, most analyses conducted here are of an exploratory nature, and while it is therefore difficult to draw up single hypotheses, following Watson et al. (1999) and Lehmann et al. (2015), the following hypotheses and predictions will be tested:

Hypothesis 1: Baboons use coping behaviours to manage their physiological stress response in aversive situations.

Hypothesis 1.1: Individuals use behavioural responses to cope with aversive situations.

Prediction 1.1i: Rates of self-directed/affiliative/agonistic behaviour increase after a predation event compared to baseline levels.

Prediction 1.1ii: Rates of self-directed/affiliative/agonistic behaviour increase during a baiting period compared to baseline levels.

Hypothesis 1.2: Behavioural responses to stressors are linked to physiological stress response measures.

a) after a predation event:

Prediction 1.2i: Changes in self-directed/affiliative/agonistic behaviour after a predation event are negatively correlated with changes in fGCM concentration.

Prediction 1.2ii: Changes in self-directed/affiliative/agonistic behaviour after a predation event are negatively linked to mean fGCM concentrations and demonstrated reactive scope.

b) during a baiting period:

Prediction 1.2iii: Changes in self-directed/affiliative/agonistic behaviour during a baiting period are negatively correlated with changes in fGCM concentration.

Prediction 1.2iv: Changes in self-directed/affiliative/agonistic behaviour during a baiting period are negatively linked to mean fGCM concentrations and demonstrated reactive scope.

Hypothesis 2: Individuals use long-term coping behaviour to manage their physiological stress response measures.

Prediction 2i: Overall rates of self-directed/affiliative/agonistic behaviour are negatively linked to mean fGCM concentrations and demonstrated reactive scope.

Hypothesis 3: Physiological stress response measures are linked to factors of sociability, reflecting social buffering.

Prediction 3i: Stronger social bonds are linked to lower mean fGCM concentrations and demonstrated reactive scope.

Prediction 3ii: Higher centrality in the affiliative social network is linked to lower mean fGCM concentrations and demonstrated reactive scope.

Prediction 3iii: Higher centrality in the agonistic social network is linked to lower mean fGCM concentrations and demonstrated reactive scope.

4.2 Methods

4.2.1 Faecal glucocorticoid metabolite concentrations and DRS

Procedures for faecal sample collection, storage, and processing are described in detail in chapter 2, section 2.2.3. Individuals' mean fGCM concentration, DRS, and DRS_{CV} were calculated based on monthly means and were only calculated for individuals for which samples from at least four months were available (n = 19 females, n = 11 males). Especially regarding the analysis of coping behaviour, depending on the event, observational and hormonal data were only available for a subset of the study subjects, so sample sizes are reported with the results. For details of the calculation of DRS and DRS_{CV}, see chapter 2, section 2.2.3.2.

4.2.2 Behavioural observations, behaviour rates and changes, and correlation of changes in behaviour and fGCM concentrations

Behavioural data were collected using continuous focal animal observations (Altmann, 1974), with details on protocols, durations, and study subjects given in chapter 2, section 2.2.1 and 2.2.2. Description of the behaviours for which overall behavioural rates were calculated and mean rates of these behaviours can be found in section 2.2.2.2.

Additionally, to investigate behavioural and hormonal responses to potentially stressful events, i.e. predation and baiting, changes in fGCM concentrations and changes in behaviour were calculated. For this purpose, a Δ behaviour or Δ fGCM concentration was calculated by subtracting the pre-event rate from the post-event rate, e.g. Δ fGCM = (post-predation fGCM) - (pre-predation fGCM). This way, a positive Δ indicates an increase in behaviour or fGCM levels after such an event compared to baseline levels.

Predation

For a comparison of behavioural rates before and after a predation event, behaviour recorded in the two weeks before a predation and in the 1.5 days after predation were compared. Data were collected on 29 individuals for the first predation event (males n = 9, females n = 20), and 28 individuals for the second predation event (males n = 9, females n = 19). Overall observation time for the first predation event was 14.52 hrs pre-predation (mean ± SD: 0.5 ± 0.24 hrs/individual) and 8.44 hrs post-predation (mean ± SD: 0.29 ± 0.08 hrs/individual), and for the second predation event 31.3 hrs pre-predation (mean ± SD: 1.12 ± 0.28 hrs/individual) and 13.82 hrs post-predation (mean ± SD: 0.49 ± 0.06 hrs/individual). As described in chapter 3, high humidity has been found to be linked to higher rates of scratching in Japanese macaques (*Macaca fuscata*; Ventura et al., 2005) and should therefore be considered in analyses of rates of self-directed behaviours. There was a significant difference in recorded humidity in the two weeks before the first predation event compared to the 1.5 days after the first predation event (Mann-Whitney U test, W = 37006, est. = 11, p < .0001, CI = 6, 16), but humidity was higher before than after the predation event and would therefore not explain an increase in this behaviour (mean(pre-predation) = 71.73%, mean(post-predation) = 61.72%). Regarding the second predation event, recorded humidity did not significantly differ between the two weeks before the predation and the 1.5 days after the predation event (Mann-Whitney U test, W = 20162, est. = 5.00, p = .182, CI = -2.00, 12), and would therefore also not explain an increase in behaviour.

When correlating changes in behaviour to changes in fGCM concentrations, faecal samples of up to one month prior to the predation event were used. While this means that behavioural and hormonal data are not strictly temporarily matched, these samples were still included to increase sample size. Even so, fGCM measures were only available for 13 individuals pre- and post-predation; for one of these individuals, samples were available for both predation events and it was therefore counted twice. If several faecal samples of one individual were available pre- or post-predation, fGCM concentrations were averaged for the pre- or post-predation period for the respective individual, and the change in concentration was then calculated.

Baiting

Behaviours recorded during the baiting period (6 days) were compared to those recorded during the three previous weeks to match durations of observations as well as possible for all individuals. Overall, 25.83 hours of observation before baiting (mean ± SD: 0.81 ± 0.21 hrs/individual) were compared with 20.06 hours during baiting (mean ± SD: 0.63 ± 0.21 hrs/individual). Data were only collected on individuals that were seen at the baiting site (males n = 12, females n = 20) which meant that two females were not included in the analysis. Focal observations during the baiting period were only conducted once the individuals had moved away from the baiting site. At the baiting site, only *ad libitum* data on agonistic interactions were recorded, for use in the dominance hierarchy calculations. Regarding humidity during this time period, recorded humidity differed significantly between the three weeks before baiting and the week of baiting (Mann-Whitney U test, W = 243360, est. = 4, p = .003, CI = 1.00, 6), but again humidity was higher in the time before the baiting period than during baiting (mean(pre-baiting) = 66.38, mean(baiting) = 62.89) and would therefore also not explain a potential increase in behaviours here.

As for the predation analysis, when investigating the link between the change in fGCM concentration and the change in behaviour, time frames for faecal samples used were longer than the time frames for observational data used. Here, faecal samples of up to six weeks prior to baiting were used whereas observational data from only three weeks prior to baiting were incorporated. Even so, fGCM measurements both before and during baiting were only available for 7 individuals. If several faecal samples were available before or during baiting for one individual, these were again averaged.

4.2.3 Measures of sociability

Composite Sociality Index

The dyadic CSI was calculated as a measure of affiliative dyadic bond strength (Silk et al., 2006a; Silk et al., 2006b) between all subject individuals. For the analysis on social buffering exploring the link between bond strength and demonstrated reactive scope and mean fGCM levels, the sum of the top three CSI values, the individual's highest CSI value, as well as their number of relatively 'weak' bonds with CSIs < 1, and their number of relatively 'strong' bonds with CSIs > 1 were used. For more detailed information, see chapter 2, section 2.2.2.2.

Social network analysis

To analyse the link between social network position in an affiliative or an agonistic network and demonstrated reactive scope and mean fGCM levels, one network was constructed based on the dyadic CSI values described above, and one network based on all agonistic interactions. Details on the construction of the networks, the calculation of network metrics, and the process of node permutation tests can be found in chapter 2, section 2.2.2.2.

4.2.4 Statistical analysis

When investigating changes in behaviour in response to certain events, all subsets of data were assessed for normality using Shapiro-Wilks tests and visual inspection of histograms. As rates of certain behaviours, such as grooming, were very low and included zeros, transformation of these data was not possible. Therefore, for all behaviours the non-parametric paired Wilcoxon signed-rank test with continuity correction was used. Here, the estimate is the (pseudo)median, i.e. the median of the differences of the pairs. Data were generally analysed separately for males and females. Throughout, 95%-CIs are reported with – in some exceptional cases – 80%- or 90%-CIs reported, due to small sample sizes and low rates of behaviours, as noted in the results. When linking changes in behaviour to changes in fGCM concentrations, distributions of all subsets approached normality, so Pearson's product-moment correlations were used. All hypothesis testing was done using two-tailed tests.

Regarding the link between long-term physiological stress response measures and changes in behaviour, overall rates of behaviour, and measures of sociability, LMs were constructed including age and rank categories as well as reproductive state for females. When investigating the link between overall physiological stress response measures and changes in behaviour in response to predation, LMMs were used including the predation event (1 or 2) as a fixed factor and subject identity as a random factor. General formulas of models are presented with the results. Where DRS or DRS_{CV} were used as response variables, these had to be $\log_2$- transformed for females to assure compliance with model assumptions. Model comparisons were based on the Information Theoretic Approach, as described in chapter 2, section 2.3. Details of the models are given in Appendix IV.

4.3 Results

4.3.1 Coping behaviour

Hypothesis 1: Baboons use coping behaviours to manage their physiological stress response in aversive situations.

Hypothesis 1.1: Individuals use behavioural responses to cope with aversive situations.

Prediction 1.1i: Rates of self-directed/affiliative/agonistic behaviour increase after a predation event compared to baseline levels.

Results of the two-tailed Wilcoxon signed-rank tests comparing behavioural rates pre- and post-predation are reported in Table 4.1. There was no significant change in any behaviour after the first predation event. For the second predation recorded, rates of scratching and total self-directed behaviour increased significantly for females, while there were trends towards increases in these behaviours for males (Figure 4.1, Figure 4.2). As scratching is part of the total self-directed behaviour measure, the increase in scratching may be driving the change in self-directed behaviour rates, so it is difficult to draw any conclusions on the other behaviours recorded here.

Table 4.1 Results of Wilcoxon signed-rank tests regarding rates of behaviour after predation compared to rates before this event. Behaviour was analysed for males and female separately and separately for each predation event (predation 1: males n = 9, females n = 20; predation 2: males n = 9, females n = 19). Significant results with p < .05 are marked in bold and underlined, statistical trends (p < 0.10) are marked by a grey background. (§ 80%-CI, ¶ 90%-CI)

		Predation 1						Predation 2					
		Scratching	Self-directed behaviour	Grooming given	Grooming received	Aggression	Agonism	Scratching	Self-directed behaviour	Grooming given	Grooming received	Aggression	Agonism
MALES	V	21	21	5	9	17	25	7	8	0	9	18	32
	est.	-2.2	-4.87	0.02	0.05	0.35	1.58	-8.05	-13.68	-0.08	-0.05	0.1	1.30
	95%-CI	-22.17, 21.49	-30.3, 27.42	-0.06, 0.3 §	-0.24, 0.19 §	-5.81, 5.71	-2.64, 7.98	-25.01, 7.15	-32.93, 3.75	-0.15, -0.02 §	-0.26, 0.14 ¶	-3.52, 7.24	-2.45, 4.87
	p	.906	.906	1	.787	.673	.363	.076	.097	.100	.834	1	.286
FEMALES	V	74	68	40	66	31	60	**33**	**35**	69	104	39	94
	est.	-5.74	-7.02	-0.04	0.04	-1.79	-1.98	**-6.40**	**-7.68**	-0.03	0.03	0.02	-0.06
	95%-CI	-16.06, 4.33	-18.1, 4.15	-0.16, 0.08	-0.24, 0.15	-5.29, 2.24	-6.20, 1.16	**-15.52, -1.44**	**-15.52, -2.43**	-0.07, 0.03	-0.06, 0.11	-2.06, 3.32	-2.55, 1.65
	p	.255	.173	.451	.755	.328	.165	**.013**	**.017**	.305	.433	1	.984

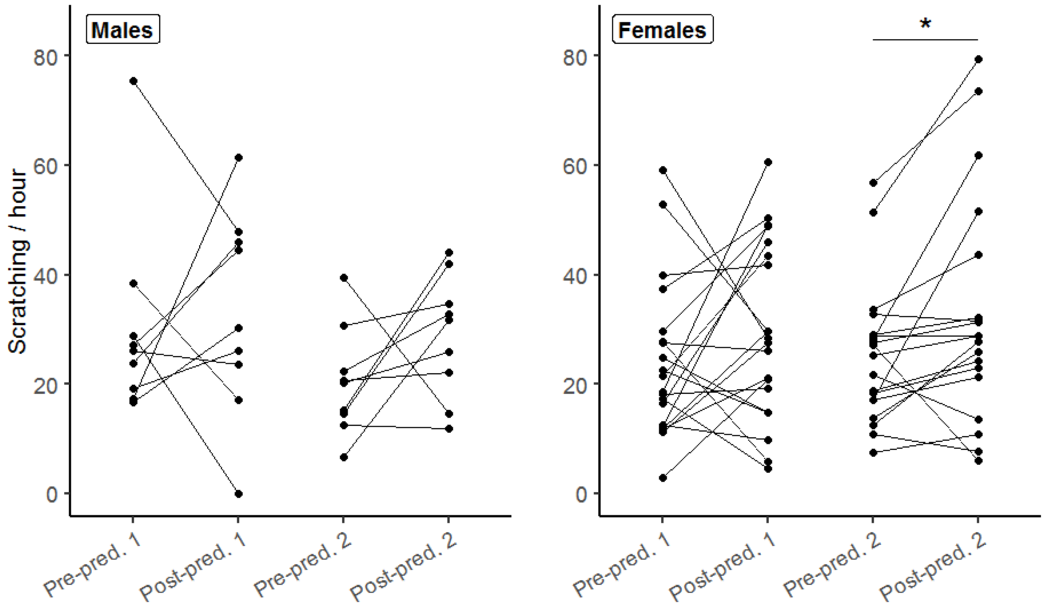


Figure 4.1 Changes in scratching rates [count of scratching/focal hour] of males (left) and females (right) after the first and second predation event. Lines join data points for individual animals. There was a statistically significant increase of scratching rates for females after the second predation event; asterisks indicate significance level: * p < .05 (V = 33, est. = -6.40, p = .013).

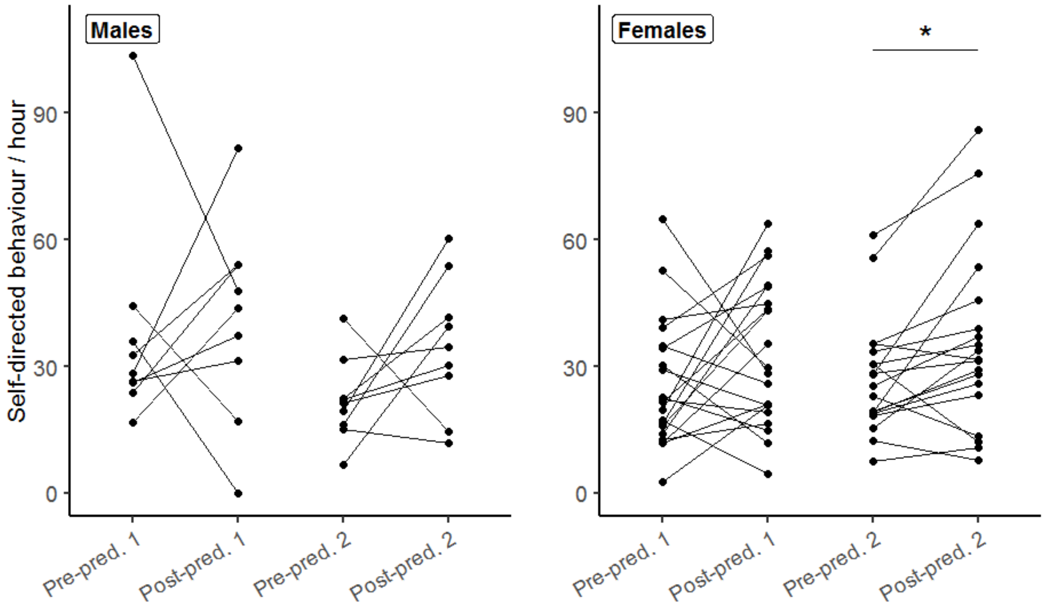


Figure 4.2 Changes in self-directed behaviour rates [count of all self-directed behaviours/focal hour] of males (left) and females (right) after the first and second predation event. Lines join data points for individual animals. There was a statistically significant increase in self-directed behaviour rates for females after the second predation event; asterisks indicate significance level: * p < .05 (V = 35, est. = -7.68, p = .017).

Prediction 1.1ii: Rates of self-directed/affiliative/agonistic behaviour increase during a baiting period compared to baseline levels.

Results of the two-tailed Wilcoxon signed-rank tests comparing rates of potential coping behaviours during a baiting period compared to baseline levels are reported in Table 4.2. Rates of scratching and rates of total self-directed behaviour increased significantly during the baiting period for males and females (Figure 4.3 and Figure 4.4). Additionally, agonism rates significantly increased during the baiting period for females (Figure 4.5).

Table 4.2 Results of Wilcoxon signed-rank tests regarding rates of behaviour during a baiting period compared to baseline levels. Behaviour was analysed separately for males and females (males: n = 12, females: n = 20). Significant results with p < .05 are marked in bold and underlined.

		Scratching	Self-directed behaviour	Grooming given	Grooming received	Aggression	Agonism
MALES	V	**1**	**6**	4	15	23	24
	est.	**-13.66**	**-11.86**	-0.03	-0.003	-2.13	-2.58
	95%-CI	**-21.52, -6.78**	**-22.82, -2.69**	-0.10, 0.01	-0.13, 0.13	-7.28, 1.86	-8.19, 1.74
	p	**.003**	**.011**	.108	.726	.224	.255
FEMALES	V	**38**	**39**	73	78	26	**39**
	est.	**-5.53**	**-6.27**	-0.02	-0.02	-1.53	**-3.55**
	95%-CI	**-14.35, -2.06**	**-15.86, -1.88**	-0.08, 0.03	-0.09, 0.05	-4.31, 0.79	**-6.40, -0.8**
	p	**.01**	**.014**	.387	.507	.184	**.014**

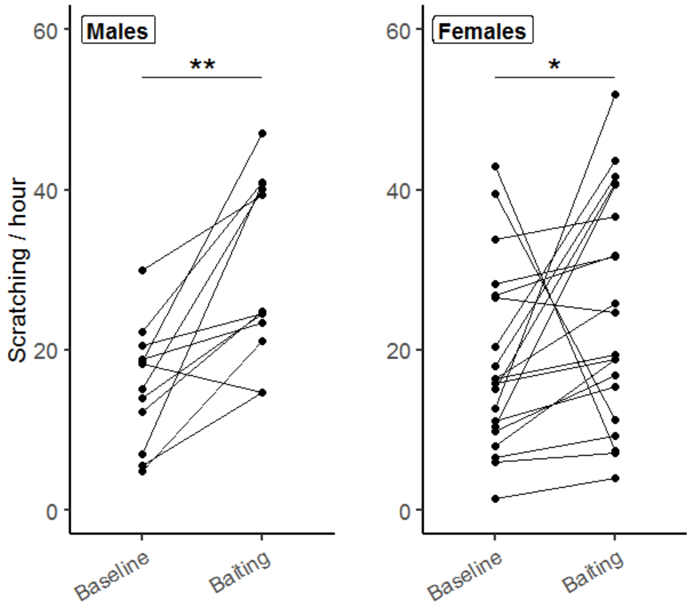


Figure 4.3 Changes in scratching rates [count of scratching/focal hour] of males (left) and females (right) during a baiting period compared to baseline levels. Lines join data points for individual animals. There was a statistically significant increase of scratching rates in males and females; asterisks indicate significance level: * p < .05; ** p < .01 (males: V = 1, est. = -13.66, p = .003; females: V = 38, est. = -5.53, p = .01).

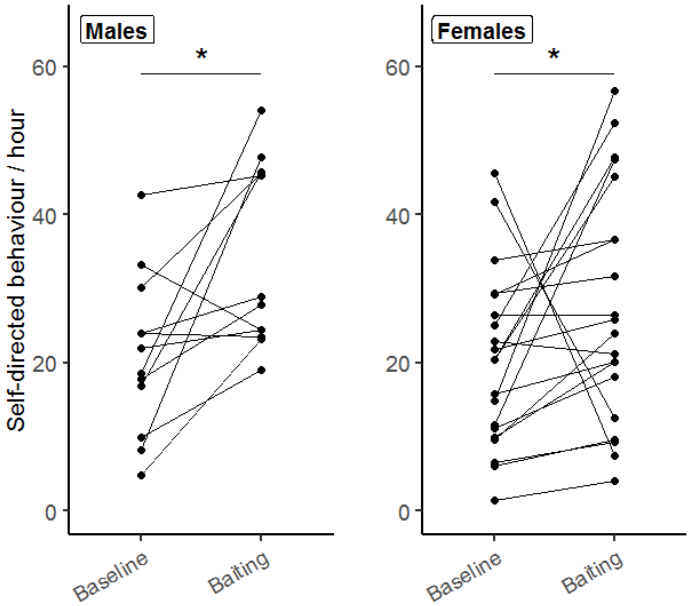


Figure 4.4 Changes in self-directed behaviour rates [count of all self-directed behaviours/focal hour] of males (left) and females (right) during a baiting period compared to baseline levels. Lines join data points for individual animals. There was a statistically significant increase of self-directed behaviour rates in both males and females; asterisks indicate significance level: * $p < .05$ (males: V = 6, est. = -11.86, $p = .011$; females: V = 39, est. = -6.27, $p = .014$).

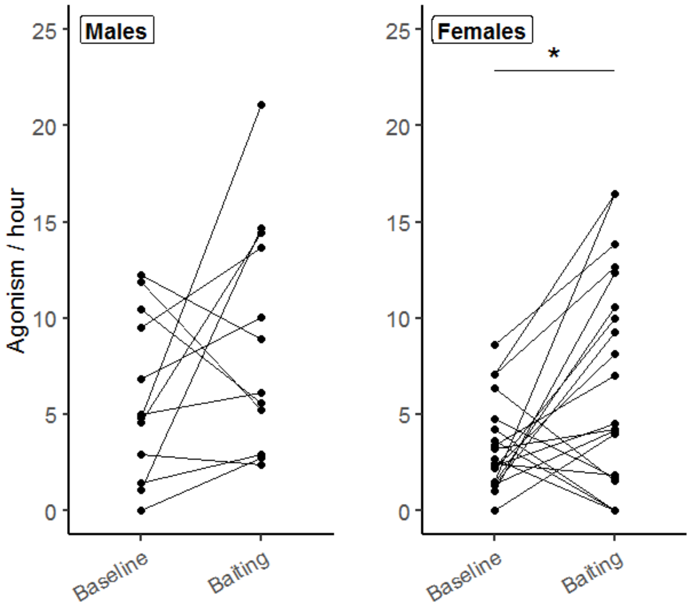


Figure 4.5 Changes in agonism rates [count of agonistic interactions/focal hour] of males (left) and females (right) during a baiting period compared to baseline levels. Lines join data points for individual animals. There was a statistically significant increase in agonism rates in females; asterisks indicate significance level: * $p < .05$ (V = 39, est. = -3.56, $p = .014$).

Hypothesis 1.2: Behavioural responses to stressors are linked to physiological stress response measures.

a) after a predation event:

Prediction 1.2i: Changes in self-directed/affiliative/agonistic behaviour after a predation event are negatively correlated with changes in fGCM concentration.

The analysis of changes in fGCM levels in response to predation in chapter 3 was conducted using longer time frames, as shown in table 3.4. This was done partially following a previous study finding increased fGCM concentrations in the month after a predation event (Engh et al., 2006a) and partially due to these months after predation events or disappearances overlapping, i.e. a female for example got killed by a leopard two weeks after a male emigrated, so baseline levels would be difficult to ascertain.

For an analysis of the link between potential coping behaviour and changes in fGCM concentration after specific events, only data on the two ascertained predation events were used. Samples from the month before the predation were averaged as baseline and compared with averaged samples representing the two days following the predation, considering the time lag until excretion, thus matching the behavioural data, for individuals for which all of these data were available (n = 13 individuals for both predation events combined). For one of these individuals, samples were available for both predation events and these were used as two data points, but data were generally assumed to be independent. Using only these samples, there was no general change in fGCM concentrations after a predation event (two-tailed paired t-test, t(13) = -0.33, est. = -69.17, p = .747, CI = -523.40, 385.06).

Even though there was no general change in fGCM concentrations when only these faecal samples were considered, the variation in the change of concentration might still be linked to changes in behaviour the animals exhibited. Therefore, Pearson's product-moment correlations were used to look for a link between the change in behaviour and a change in fGCM concentrations. There was no significant correlation between Δ fGCM and the change in any of the six behaviours (Table 4.3).

Table 4.3 Results of Pearson's product-moment correlations regarding links between changes in behaviour rates and changes in fGCM concentrations after predation events. Data were analysed for males and female together (n = 14), statistical trends with p < .1 are marked by a grey background.

		Scratching	Self-directed behaviour	Grooming given	Grooming received	Aggression	Agonism
MALES & FEMALES	t	1.10	1.21	-0.63	-1.25	-1.89	-1.52
	df	12	12	12	12	12	12
	r	0.30	0.33	-0.18	-0.34	-0.48	-0.40
	95%-CI	-0.27, 0.72	-0.24, 0.73	-0.65, 0.39	-0.74, 0.23	-0.81, 0.07	-0.77, 0.16
	p	.291	.25	.543	.235	.083	.154

Prediction 1.2ii: Changes in self-directed/affiliative/agonistic behaviour after a predation event are negatively linked to mean fGCM concentrations and demonstrated reactive scope.

To investigate whether the observed changes in behaviour after predation events were associated with individuals' mean physiological stress response levels or their demonstrated reactive scope, separate models were constructed, with each potential coping behaviour as a response variable. For each behaviour, models containing one of DRS, DRS$_{CV}$, mean fGCM concentration, or the dyadic CSI to the killed individual were compared to a null model, which only included age, rank category, predation event 1 or 2, and reproductive state at the time for females. Full result tables are shown in Appendix IV-I.

Table 4.4 gives an overview of the results of the model comparisons. In several cases, single observations or individuals were highly influential data points, i.e. Cook's distance > 1. In these cases, the respective models were run again without the influential data point and compared again to the new null model. Results of these comparisons are added in brackets below the overall model results, and details of the models can also be found in Appendix IV-I.

For males, there was high multicollinearity in all mean fGCM models between the mean fGCM concentration and rank (i.e. VIF > 2), so that rank category was excluded from these models. Besides the null models, all mean fGCM models subsequently received substantial support in the model comparisons. This likely reflects the finding of multicollinearity, as apparently mean fGCM concentrations varied with rank category to a certain degree and thus models either including rank category or mean fGCM concentration received support in the model comparison. Based on the principle of parsimony, though, null models should be regarded as the better models if there is no convincing evidence to the contrary as they represent the simpler explanation. Regarding the change in scratching rates, the DRS_{CV} model also received some support in addition to the null model, once the influential data point was removed. While here Δ AIC_C was 2.92 and thus larger than 2, the DRS_{CV} model explained nearly 20% more of the variation than the null model did. Males with higher DRS_{CV} values tended to decrease their scratching rates, whereas males with lower DRS_{CV} values tended to increase their scratching rates after predation events (Figure 4.6). In the case of changes in rates of giving grooming, the CSI model was clearly the best model of the set when all data were considered, but when the influential point was removed, only the null and mean fGCM models received substantial support. This indicates that the one male who had the highest dyadic CSI with the killed female showed a strong decrease in his grooming behaviour, but that otherwise CSI was not necessarily linked to changes in grooming behaviour (Figure 4.7). Similarly, the CSI model received substantial support in predicting changes in agonism rates, but when the influential data point was removed the Δ AIC_C was again > 2 compared to the null model. Here it should be noted, though, that the effect size of the CSI model was still by far the largest of all models, with the CSI explaining nearly an additional 20% compared to the null model even when the male with the high dyadic CSI was removed. Generally, CSI was a positive predictor of changes in agonistic behaviour, as only males with higher dyadic CSI values to the killed individual showed an increase in agonistic behaviour (Figure 4.7).

For females, both DRS and DRS_{CV} models received substantial support, in addition to the null models, in explaining changes in scratching and total self-directed behaviour rates, and full models also explained 5% - 10% more of the variation in behaviour than the null models did. Even though graphical visualisation does not reveal a very clear relationship, both DRS and DRS_{CV} were positive predictors of changes in scratching (Figure 4.8) and self-directed behaviour (Figure 4.9). Additionally, the mean fGCM model received support in predicting the change in rates of giving grooming, even though it was not able to explain more of the variation than the null model already did. Regarding the rates of agonistic interactions, once the influential data point was removed, both the DRS_{CV} and the mean fGCM models also received substantial support, explaining an additional 8% of variation in the change of behaviour, but estimates are relatively low (Figure 4.10).

Besides the variables in question, some other control factors seemed to be linked to changes in females' behaviour after predation events. There was some support for an effect of rank category on changes in rates of giving grooming, in that lower-ranking females tended to have stronger increases in grooming rates than high-ranking females

(Figure 4.11; Appendix IV-I). Furthermore, reproductive state was predictive of changes in aggression: both pregnant and lactating females tended to increase their rates of aggression after predation more strongly than cycling females did, but these results should be considered with caution as only four data points for cycling females were available (Appendix IV-I). Moreover, once one influential data point in the analysis of changes in agonism rates was removed, age was a significant predictor of changes in agonism, in that younger females showed stronger increases in agonistic behaviour after predation events than middle- or old-aged females did (Figure 4.11; Appendix IV-I).

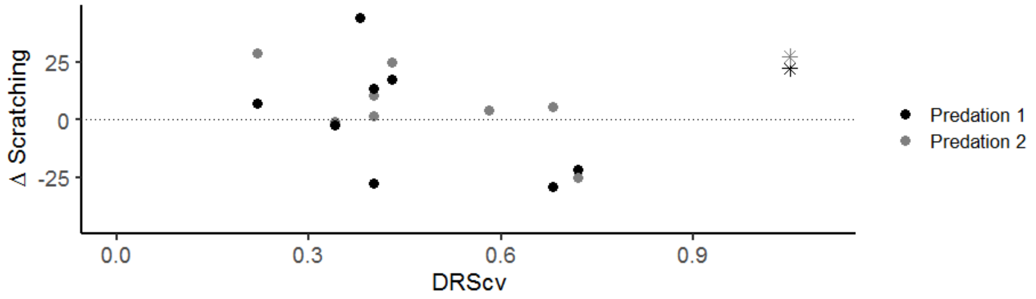


Figure 4.6 Changes in males' scratching rates [count of scratching/focal hour] after predation events in relation to demonstrated reactive scope measured as DRS_{CV} (with the influential data points (marked *), Δ AIC_C = 5.51 and R^2 = 22.30%; without the influential data points, Δ AIC_C = 2.92 and R^2 = 42.58%).

Male LMM: *Δ behaviour ~ stress measure or CSI + age class + rank category + predation event + (1|individual)*

Female LMM: *Δ behaviour ~ stress measure or CSI + age class + rank category + reproductive state + predation event + (1|individual)*

Table 4.4 Results of LMM comparisons regarding the change in behaviour after a predation event, using demonstrated reactive scope (DRS and DRS$_{CV}$), mean fGCM concentrations, and the dyadic CSI to the killed individual as predictors. Models included age, rank category, predation event 1 or 2, and for females, reproductive state at the time. Models with a Δ AIC$_C$ < 2 or strikingly large effect sizes were considered to have received substantial support and are marked in bold and underlined. Numbers in brackets represent model comparison results once influential data points (Cook's distance > 1) were removed.

	MALES										FEMALES									
	Predictor: (Δ AIC$_C$, marginal R^2 [%])																			
Response:	**DRS model**		**DRS$_{CV}$ model**		**fGCM model**		**CSI model**		**null model**		**DRS model**		**DRS$_{CV}$ model**		**fGCM model**		**CSI model**		**null model**	
Δ behaviour	**Δ AIC$_C$**	**R^2**	**Δ AIC$_C$**	**R^2**	**Δ AIC$_C$**	**R^2**	**Δ AIC$_C$**	**R^2**	**Δ AIC$_C$**	**R^2**	**Δ AIC$_C$**	**R^2**	**Δ AIC$_C$**	**R^2**	**Δ AIC$_C$**	**R^2**	**Δ AIC$_C$**	**R^2**	**Δ AIC$_C$**	**R^2**
Δ scratching	4.83	26.96	5.51 **(2.92**	22.30 **42.58)**	**1.85**	**8.81**	5.16	22.36	**0** **(0**	**22.05** **24.35)**	**1.38**	**15.05**	**0**	**18.23**	3.5	9.92	3.65	9.54	**0.23**	**9.29**
Δ self-directed behaviour	4.82	20.87	5.51	16.77	**1.32**	**8.34**	5.28	17.52	**0**	**16.52**	**1.5**	**17.93**	**0**	**21.26**	4.19	11.59	3.97	12.13	**0.86**	**11.13**
Δ giving grooming	18.89 (4.72	21.20 20.74)	19.73 (3.5	17.27 26.51)	15.06 **(0**	12.87 **14.00)**	**0** (5.83	**73.23** 15.13)	14.8 **(0.06**	14.18 **13.68)**	2.51	15.48	2.79	14.77	**1.27**	**18.51**	3.22	22.94	**0**	**21.83**
Δ receiving grooming	5.56 (5.83	10.42 28.65)	5.47 (5.83	10.89 28.49)	**0.08** **(0.96**	**10.01** **20.82)**	3.89 (5.47	18.73 30.60)	**0** **(0**	**10.42** **27.28)**	3.36	9.24	3.37	9.23	3.51	8.85	2.05	12.3	**0**	**8.81**
Δ aggression	5.46	2.77	5.35	3.43	**0.06**	**1.86**	3.09	15.38	**0**	**2.21**	3.52 (2.81	18.64 42.83)	3.44 (2.77	18.18 42.66)	3.24 (3.64	18.6 41.76)	3.01 (2.65	21.11 44.75)	**0** **(0**	**18.57** **41.69)**
Δ agonism	5.89	4.63	5.92	4.49	**0.69**	**2.59**	**0** **(2.25**	**32.3** **27.11)**	**0.6** **(0**	**3.07** **7.77)**	3.52 (2.1	12.89 27.71)	3.41 **(0**	13.16 **32.14)**	3.52 **(0.88**	12.89 **30.26)**	3.29 (2.82	13.45 24.28)	**0** **(0.11**	**12.89** **24.28)**

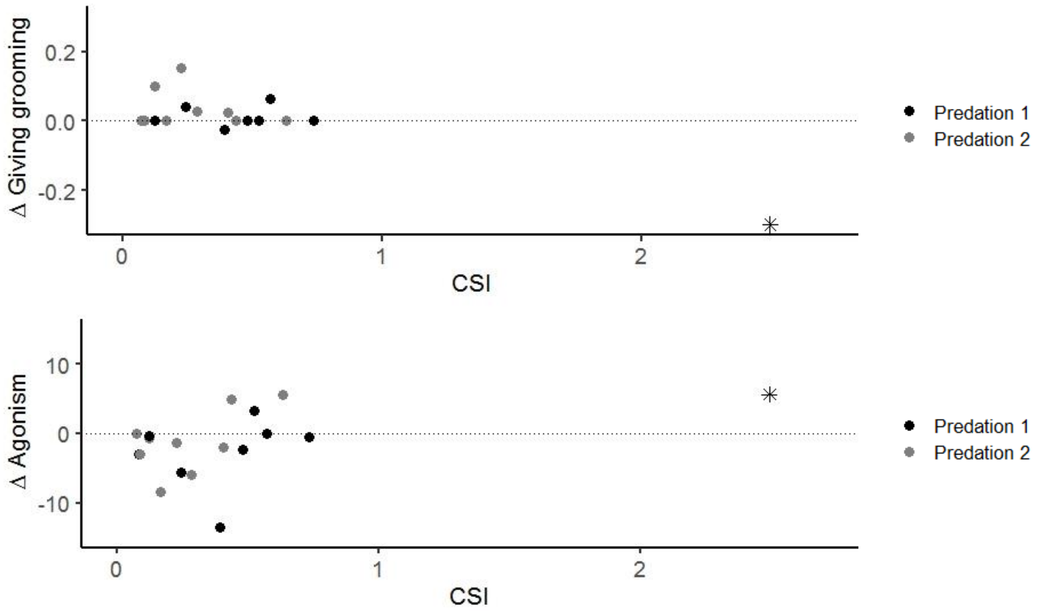


Figure 4.7 Changes in males' rates of giving grooming [duration of grooming in hours/focal hour] at the top, and rates of agonism [count of agonistic interactions/focal hour] at the bottom after predation events in relation to dyadic CSI to the killed individual (with the influential data point (marked *), Δ giving grooming: $\Delta\ \mathrm{AIC_C} = 0$ and $R^2 = 73.23\%$; Δ agonism: $\Delta\ \mathrm{AIC_C} = 0$ and $R^2 = 32.3\%$; without the influential data point, Δ giving grooming: $\Delta\ \mathrm{AIC_C} = 5.83$ and $R^2 = 15.13\%$; Δ agonism: $\Delta\ \mathrm{AIC_C} = 2.25$ and $R^2 = 27.11\%$).

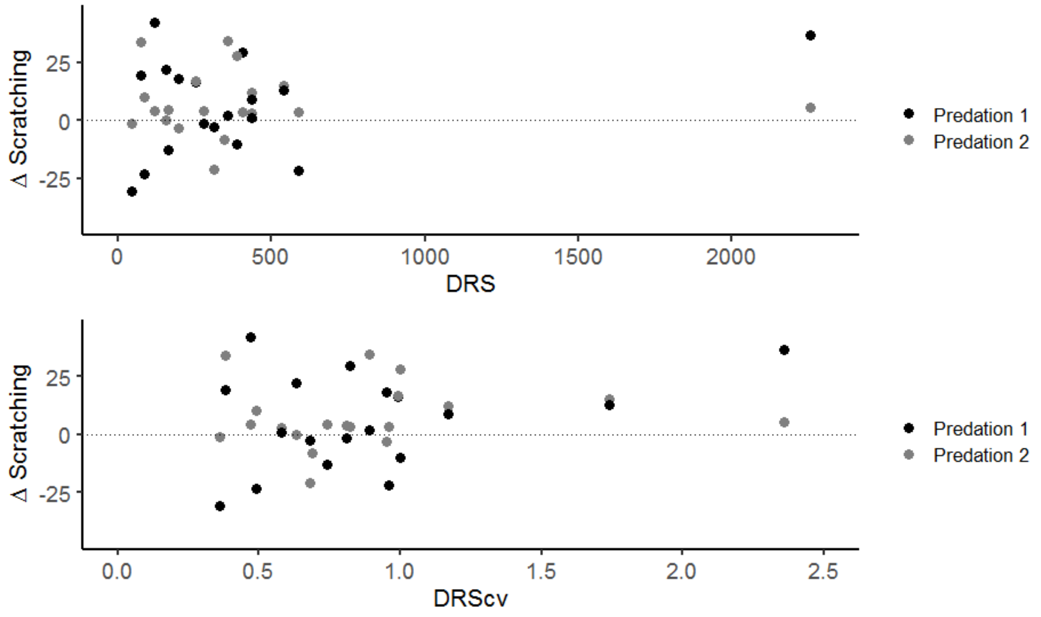


Figure 4.8 Changes in females' scratching rates [count of scratching/focal hour] after predation events in relation to demonstrated reactive scope measured as DRS (top) and $\mathrm{DRS_{CV}}$ (bottom) (DRS: $\Delta\ \mathrm{AIC_C} = 1.38$ and $R^2 = 15.05\%$; $\mathrm{DRS_{CV}}$: $\Delta\ \mathrm{AIC_C} = 0$ and $R^2 = 18.23\%$).

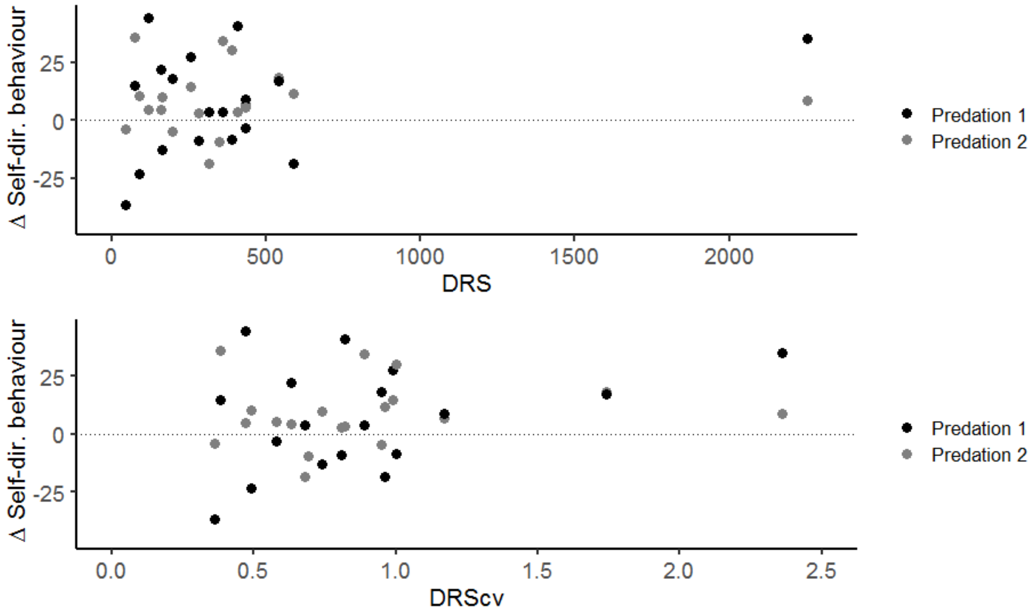


Figure 4.9 Changes in females' self-directed behaviour rates [count of all self-directed behaviours/focal hour] after predation events in relation to demonstrated reactive scope measured as DRS (top) and DRS_{CV} (bottom) (DRS: Δ AIC_C = 1.5 and R^2 = 17.93%; DRS_{CV}: Δ AIC_C = 0 and R^2 = 21.26%).

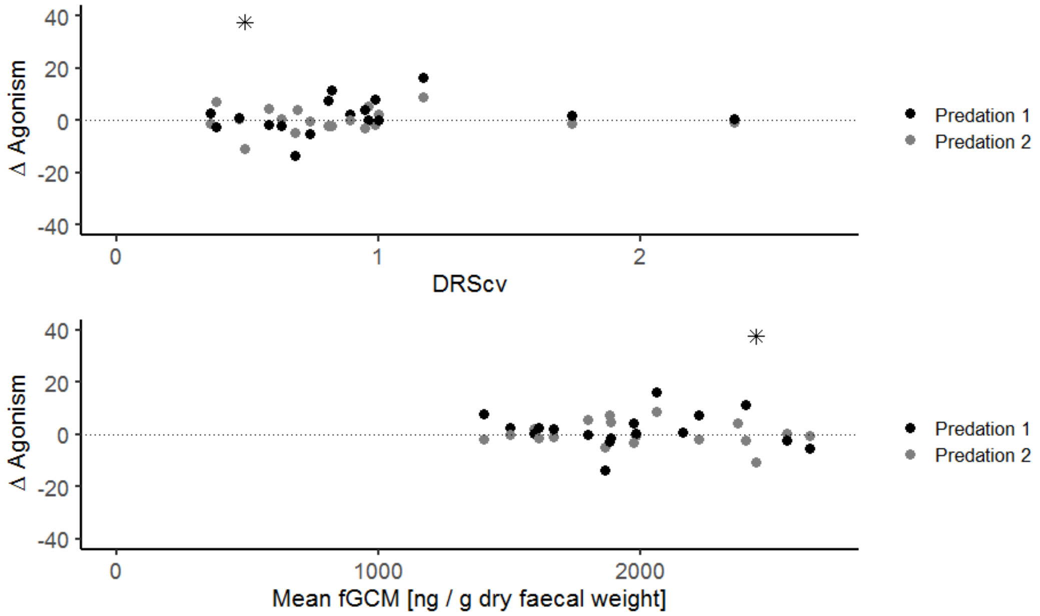


Figure 4.10 Changes in females' agonism rates [count of agonistic interactions/focal hour] after predation events in relation to demonstrated reactive scope measured as DRS_{CV} (top) and mean fGCM concentration (bottom) (with the influential data point (marked *), DRS_{CV}: Δ AIC_C = 3.41 and R^2 = 13.16%; mean fGCM: Δ AIC_C = 3.52 and R^2 = 12.89%; without the influential data point, DRS_{CV}: Δ AIC_C = 0 and R^2 = 32.14%; mean fGCM: Δ AIC_C = 0.88 and R^2 = 30.26%).

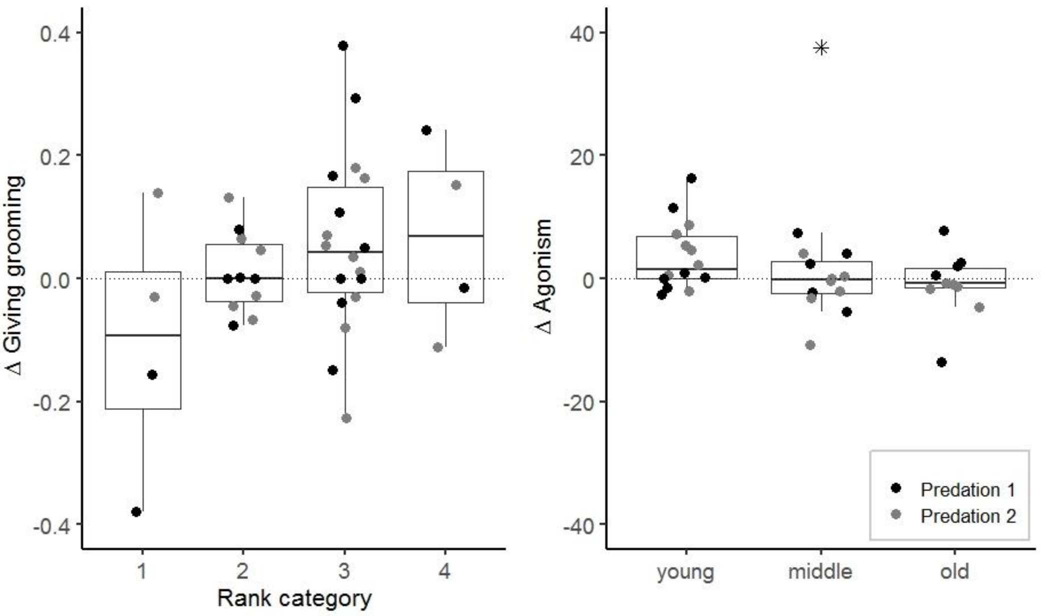


Figure 4.11 Changes in females' rates of giving grooming [duration of grooming in hours/focal hour] after predation events by rank category (left) and change in females' agonism rates [count of agonistic interactions/focal hour] by age class on the right. Boxes represent IQR, horizontal line shows the median, and whiskers go out to 1.5x the IQR or the furthest point within this range, with outliers being plotted outside of the whiskers (Δ giving grooming, rank: est. ± SE = 0.05 ± 0.03, p = .09; Δ agonism, with influential data point (marked *), age: est. ± SE = -2.48 ± 1.62, p = .134; without influential data point, age: est. ± SE = -2.38 ± 1.11, p = .020. All estimates taken from null models).

Hypothesis 1.2: Behavioural responses to stressors are linked to physiological stress response measures.

b) during a baiting period:

Prediction 1.2iii: Changes in self-directed/affiliative/agonistic behaviour during a baiting period are negatively correlated with changes in fGCM concentration.

It was assumed that fGCM concentrations would increase during the baiting period due to the sudden contest competition and heightened levels of aggression at the bait site. However, a two-tailed paired t-test showed no significant change in fGCM concentrations (two-tailed paired t-test, n = 7, t(6) = 1.96, est. = 745.23, p = .097, CI = -183.1, 1673.56).

To investigate whether the changes found in behavioural rates during baiting were linked to changes in fGCM concentration, Pearson's product-moment correlations were conducted investigating the link between changes in each of the six behaviours and Δ fGCM, and results are presented in Table 4.5. Correlations were not statistically significant for any of the behaviours.

Table 4.5 Results of Pearson's product-moment correlations regarding links between changes in behaviour rates and changes in fGCM concentrations during a baiting period. Data were analysed for males and female combined (n = 7), statistical trends with p < .1 are marked by a grey background.

		Scratching	Self-directed behaviour	Grooming given	Grooming received	Aggression	Agonism
MALES & FEMALES	t	0.88	1.00	-1.72	-0.06	-1.65	-2.53
	df	5	5	5	5	5	5
	r	0.37	0.41	-0.61	-0.03	-0.6	-0.75
	95%-CI	-0.53, 0.88	-0.5, 0.88	-0.93, 0.26	-0.76, 0.74	-0.93, 0.29	-0.96, 0.01
	p	.42	.363	.145	.958	.159	.053

Prediction 1.2iv: Changes in self-directed/affiliative/agonistic behaviour during a baiting period are negatively linked to mean fGCM concentrations and demonstrated reactive scope.

To investigate whether demonstrated reactive scope or mean physiological stress response levels were linked to changes in behaviour during the baiting period, LMs were constructed including one of DRS, DRS_{CV} or mean fGCM, as well as age and rank category, and the models compared to a null model only including age and rank category. All analyses were done for males and females separately, with female models also including reproductive state at the time of baiting. An overview of the results of model comparisons is presented in Table 4.6, while details of the full models can be found in Appendix IV-I.

Neither demonstrated reactive scope, measured as DRS or DRS_{CV}, nor mean fGCM concentrations were linked to changes in behaviour of males during baiting, as the null models were in all cases the best models.

For females, however, there was some support for the mean fGCM models of scratching and self-directed behaviour, even though there were some problems with the model assumptions, as there was no homoscedasticity of residuals for the scratching model. For these models, the Δ AIC_C was < 2 and effect sizes about 15% larger than those of the null models: females with higher mean fGCM concentrations increased their rates of scratching and other self-directed behaviours more strongly during baiting than females with lower mean fGCM concentrations did (Figure 4.12), in contrast to the prediction. For all other behaviours, the null models were the best models.

While there was no evidence for a link between demonstrated reactive scope or mean fGCM level and changes in male behaviour during baiting, age and rank category were significant predictors of some of these changes: rank category predicted changes in scratching (and total self-directed behaviour) rates, in that high-ranking males showed a stronger increase in these behaviours than lower-ranking males (Appendix IV-I; Figure 4.13). Additionally, changes in giving and receiving grooming seemed to be influenced by rank, and to a small degree by age, as well (Appendix IV-I), in that low-ranking males increased their grooming during the baiting period, whereas high-ranking males received more grooming (Figure 4.14). While these results need to be considered carefully, as single individuals might have a large effect due to low rates of change, the large effect sizes of the null models suggest some predictive power here. Neither age nor rank was predictive of aggression or agonism rates for males, as comparatively low effect sizes of the null models suggest.

For females, there was statistical evidence that changes in giving grooming were influenced by reproductive state, rank category, and age class (Appendix IV-I). Regarding reproductive state, most pregnant females decreased their rate of giving grooming, while most lactating females increased them (Figure 4.15); regarding age classes, while there was no clear change for young and middle-aged females, all older females increased their rates of giving grooming (Figure 4.15); considering rank category, visual inspection suggests that this effect was probably due to the two females of rank category 1 decreasing their rates, as there was no clear difference between the other rank categories (Figure 4.16). Rank category was, however, a clear significant predictor of changes in aggressive behaviour (Appendix IV-I), with high-ranking females showing a stronger increase in aggressive behaviour than lower-ranking females (Figure 4.16).

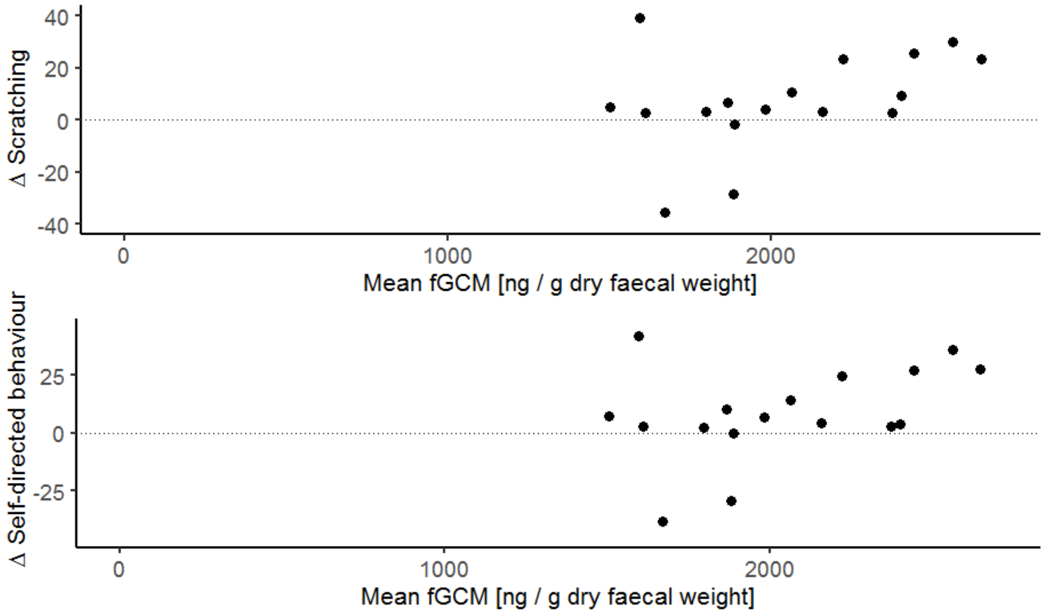


Figure 4.12 Changes during a baiting period in females' scratching rates [count of scratching/focal hour] at the top and changes in females' rates of self-directed behaviour [count of all self-directed behaviours/focal hour] at the bottom, in relation to mean fGCM concentrations [ng/g dry faecal weight] (Δ scratching: Δ AIC_C = 1 and R^2 = 39.8%; Δ self-directed behaviour: Δ AIC_C = 1.1 and R^2 = 37.79%).

Male LM: *Δ behaviour ~ stress measure + age class + rank category*

Female LM: *Δ behaviour ~ stress measure + age class + rank category + reproductive state*

Table 4.6 Results of LM comparisons regarding the change in behaviour during a baiting period, using demonstrated reactive scope (DRS and DRS$_{CV}$) and mean fGCM concentrations as predictors. Models included age, rank category, and for females, reproductive state at the time. Models with a Δ AIC$_C$ < 2 were considered to have received substantial support and are marked in bold and underlined.

	MALES								FEMALES							
	Predictor: (Δ AIC$_C$, marginal R^2 [%])															
	DRS model		**DRS$_{CV}$ model**		**fGCM model**		**null model**		**DRS model**		**DRS$_{CV}$ model**		**fGCM model**		**null model**	
Response: Δ behaviour	**Δ AIC$_C$**	**R^2**	**Δ AIC$_C$**	**R^2**	**Δ AIC$_C$**	**R^2**	**Δ AIC$_C$**	**R^2**	**Δ AIC$_C$**	**R^2**	**Δ AIC$_C$**	**R^2**	**Δ AIC$_C$**	**R^2**	**Δ AIC$_C$**	**R^2**
Δ scratching	3.35	62.58	5.92	54.09	6.35	52.51	**0**	**52.07**	6.02	22.38	6.05	22.28	**1**	**39.8**	**0**	**23.82**
Δ self-directed behaviour	6.14	53.37	7.1	49.75	6.11	53.46	**0**	**52.16**	6.03	21.98	6.04	21.91	**1.1**	**37.79**	**0**	**23.44**
Δ grooming given	5.46	54.04	4.35	57.90	7.31	46.96	**0**	**50.21**	5.99	45.43	4.84	48.41	5.81	45.90	**0**	**47.45**
Δ grooming received	7.29	49.55	7.04	50.52	6.79	51.44	**0**	**52.71**	5.7	30.25	5.65	30.41	4.9	32.77	**0**	**30.97**
Δ aggression	7.33	0.05	7.18	1.01	6.24	6.88	**0**	**0.05**	4.46	33.41	4.3	33.9	5.6	29.80	**0**	**30.15**
Δ agonism	6.93	15.9	7.27	13.94	7.06	15.16	**0**	**15.25**	6.04	30.08	4.32	35.46	5.85	30.70	**0**	**31.94**

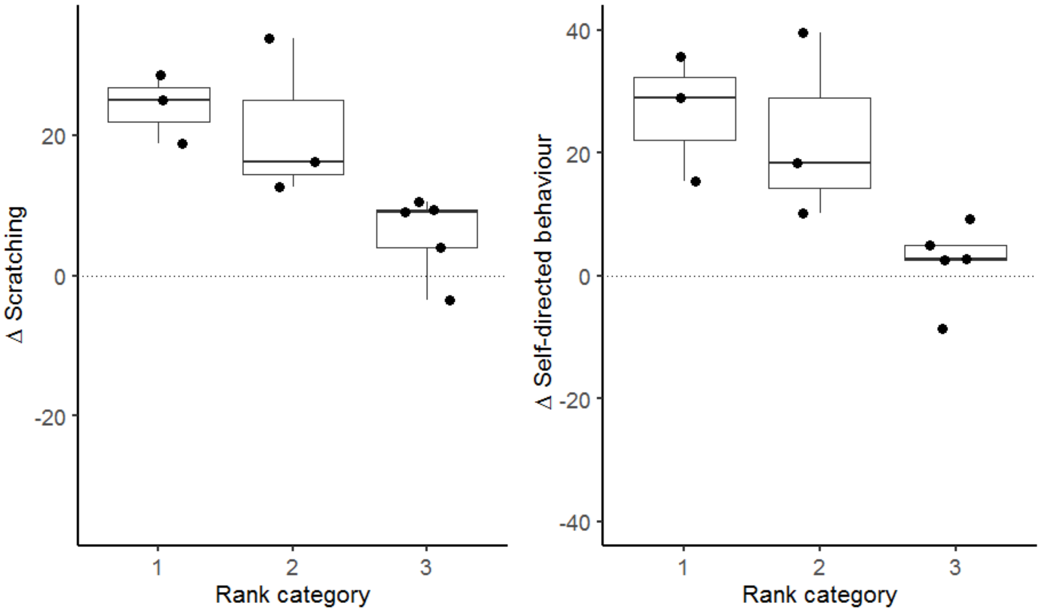


Figure 4.13 Changes during a baiting period in males' scratching rates [count of scratching/focal hour] on the left and changes in males' self-directed behaviour rates [count of all self-directed behaviours/focal hour] on the right, in relation to rank category (Δ scratching, rank: est. ± SE = -9.68 ± 3.27, p = .018; Δ self-directed behaviour, rank: est. ± SE = -14.07 ± 4.46, p = .013. All estimates taken from null models).

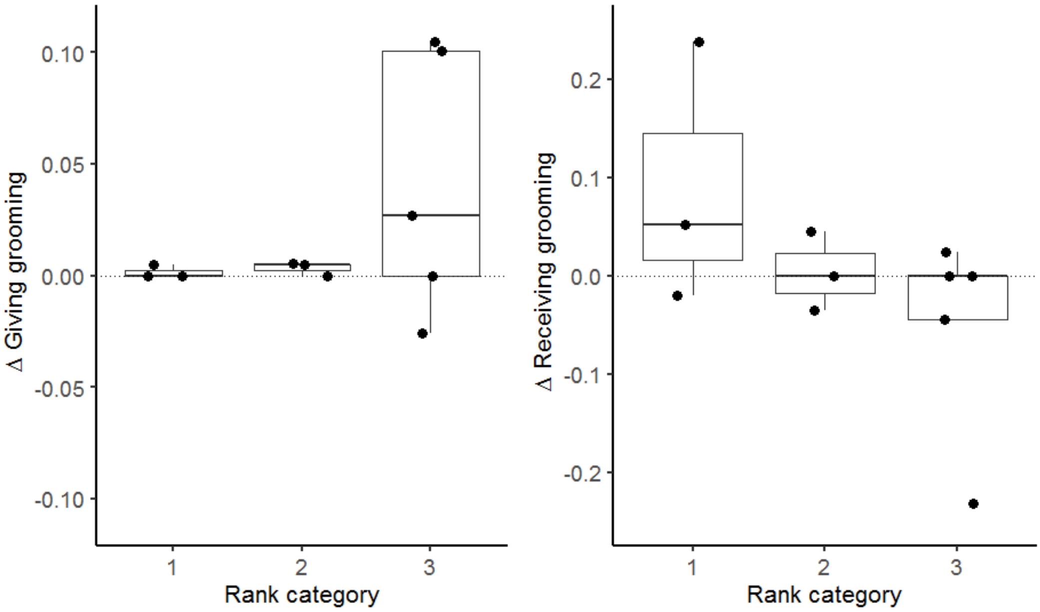


Figure 4.14 Changes during a baiting period in males' rates of giving grooming on the left, and rates of receiving grooming on the right [duration of grooming in hours/focal hour] in relation to rank category (Δ giving grooming, rank: est. ± SE = 0.04 ± 0.01, p = .022; Δ receiving grooming, rank: est. ± SE = -0.10 ± 0.03, p = .013. All estimates taken from null model).

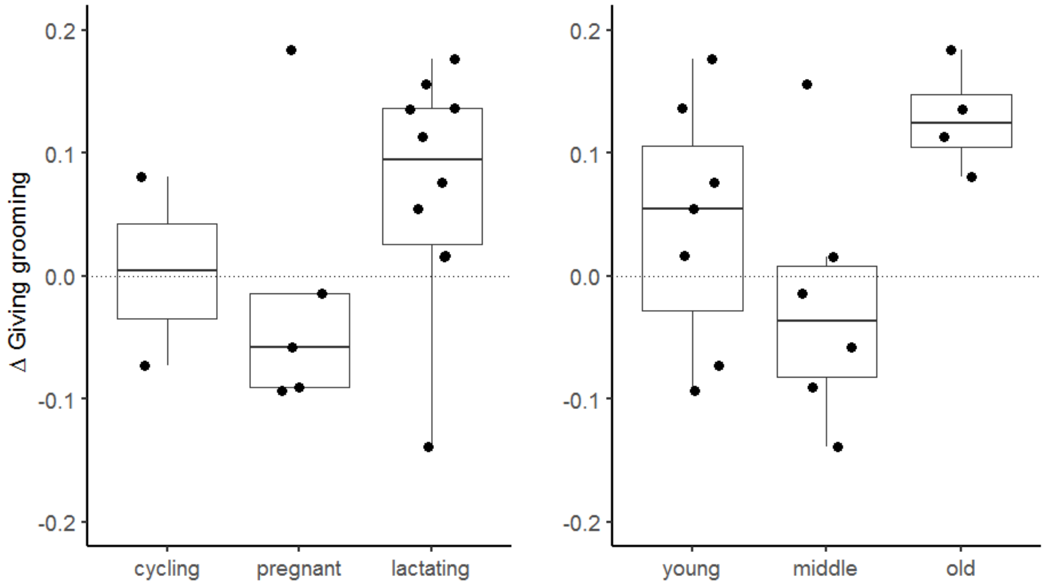


Figure 4.15 Changes during a baiting period in females' rates of giving grooming [duration of grooming in hours/focal hour] in relation to reproductive state (left) and age class (right) (reproductive state: cycl. – preg.: est. ± SE = 0.07 ± 0.08, p = .364; cycl. – lact.: est. ± SE = -0.19 ± 0.07, p = .026; age: est. ± SE = 0.07 ± 0.03, p = .026. All estimates taken from null model).

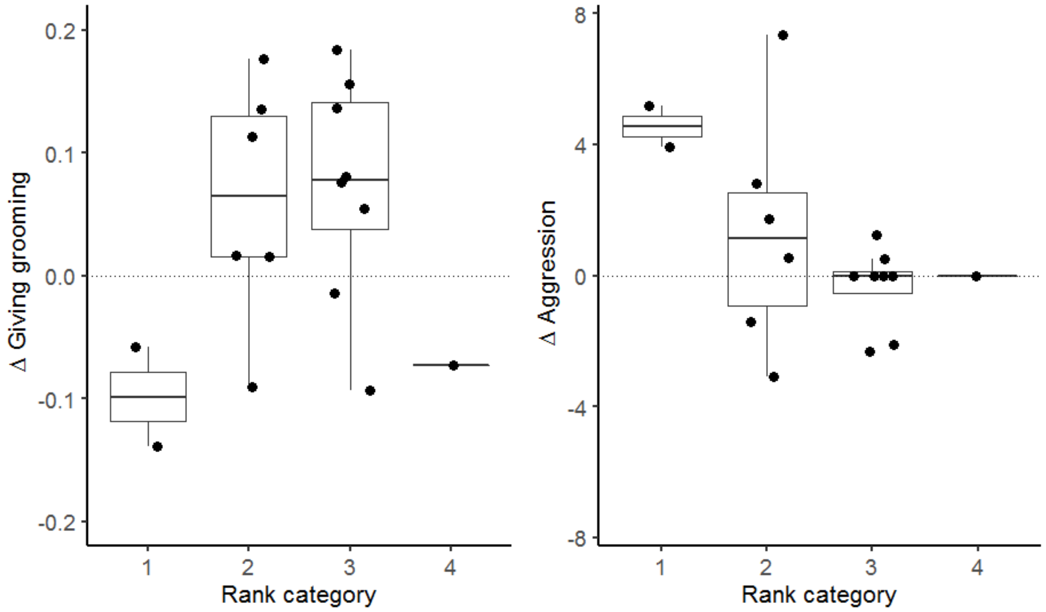


Figure 4.16 Changes during a baiting period in females' rates of giving grooming [duration of grooming in hours/focal hour] on the left and changes in females' rates of aggression given [count of aggression/focal hour] on the right, in relation to rank category (Δ grooming given, rank: est. ± SE = 0.08 ± 0.03, p = .021; Δ aggression, rank: est. ± SE = -2.22 ± 0.96, p = .039. All estimates taken from null models).

4.3.2 Long-term coping behaviour

Hypothesis 2: Individuals use long-term coping behaviour to manage their physiological stress response measures.

Prediction 2i: Overall rates of self-directed/affiliative/agonistic behaviour are negatively linked to mean fGCM concentrations and demonstrated reactive scope.

Coping behaviours, besides being purely shown in response to a stressor, might also be used to mitigate an individual's physiological stress response. Therefore, it was investigated whether overall rates of potential coping behaviours are (negatively) linked to either demonstrated reactive scope or mean fGCM concentrations measured over the whole study period. Data were analysed for males and females separately, and for females both DRS and DRS_{CV} values had to be $\log_2$-transformed for the models to comply with linear model assumptions. For each potential coping behaviour, i.e. scratching, self-directed behaviour, giving and receiving grooming, aggression, and agonism, a separate model was constructed, and all compared to a null model including age and rank category. Overall results of model comparisons are compiled in Table 4.7, and model details are presented in Appendix IV-II.

For males, there was high multicollinearity between giving grooming and rank so that rank was excluded from these models. As Table 4.7 shows, the models including giving grooming received substantial support in explaining variation in DRS, DRS_{CV}, and mean fGCM levels in addition to the null models, but only regarding DRS_{CV} did the giving grooming model have a larger effect size than the null model, if only by 1%. As there was a high multicollinearity between rank and giving grooming, an exploratory analysis was conducted into this relation, finding that rank category explained nearly 40% of variation in grooming rates of males (Appendix IV-II), even though rank categories did not differ significantly in their mean rates of giving grooming (Table 4.8). These results indicate that high rates of giving grooming might be linked to lower demonstrated reactive scope, and potentially mean fGCM concentrations, as predicted and that this link might be rank-dependent as shown in Figure 4.17. There was no support for an effect of any of the other behaviours.

For females, there was high multicollinearity for both rates of aggression and rates of agonism with rank category, thus rank was excluded from these models. Here, the aggression model was the best model for both DRS and DRS_{CV} (Table 4.7, Figure 4.18) with substantial support for the agonism and null models as well, even though all explained only a relatively small part of the variation in demonstrated reactive scope. Based on the high multicollinearity, the link between aggression rates and rank category was also investigated, with rank category explaining over 60% of variation in female aggression rates (Appendix IV-II). Comparison of mean aggression rates between rank categories showed that females in rank categories 1 and 2 had higher mean aggression rates than females in rank categories 3 and 4, but there was no difference between the two high- or between the two low-rank categories themselves (Table 4.8, Figure 4.18). As was the case for males, this indicates that the link between aggression as a potential coping behaviour and demonstrated reactive scope might be rank-dependent, as high-ranking females showed substantially higher rates of aggression than low-ranking females and, as predicted, seemed to have lower scores of DRS and DRS_{CV} the higher their rates of aggression were (Figure 4.18), although a larger sample size would probably be needed for conclusive statistical evidence. Interestingly, while high-ranking females showed aggression at higher rates, lower ranking females did not receive aggression at higher rates than high-ranking females did (Table 4.8). There was no support for a link between any other behaviour and demonstrated reactive scope. Regarding mean fGCM concentrations, the null model was the best model and there was no substantial support for an association between any of the behaviours and mean fGCM concentrations of females based on model comparisons.

LM: *stress measure ~ behaviour rate + age class + rank category*

Table 4.7 Results of LM comparisons regarding the link between long-term rates of behaviour and demonstrated reactive scope (DRS and DRS_{CV}) and mean fGCM concentrations of males and females. Models included age and rank category; DRS and DRS_{CV} values of females were log_2-transformed. Models with a $\Delta AIC_C < 2$ were considered to have received substantial support and are marked in bold and underlined.

	MALES						FEMALES					
	Response variable: (ΔAIC_C, marginal R^2 [%])											
	DRS		**DRS_{CV}**		**mean fGCM**		**DRS**		**DRS_{CV}**		**mean fGCM**	
Predictor behaviour:	**ΔAIC_C**	**R^2**	**ΔAIC_C**	**R^2**	**ΔAIC_C**	**R^2**	**ΔAIC_C**	**R^2**	**ΔAIC_C**	**R^2**	**ΔAIC_C**	**R^2**
scratching	7.11	31.06	7.4	8.79	6.39	23.99	3.14	7.96	4.49	10.92	2.43	40.07
self-directed behaviour	7.33	29.93	7.22	9.85	6.26	24.67	3.25	7.51	4.74	9.92	2.68	39.35
grooming given	**1.28**	**25.76**	**0**	**10.34**	**1.17**	**13.61**	4.89	0.57	5.5	6.81	2.31	40.41
grooming received	7.33	29.92	7.51	8.1	6.84	21.55	4.06	4.15	4.82	9.47	3.72	36.3
aggression	5.97	36.53	6.06	16.66	5.63	27.95	**0**	**5.75**	**0**	**14.59**	3.55	25.92
agonism	5.24	39.98	5.06	22.17	6.06	25.75	**0.51**	**3.45**	**0.5**	**12.55**	6.45	14.87
null model	**0**	**32.80**	**0.19**	**9.11**	**0**	**20.99**	**1.2**	**0.28**	**1.77**	**7.11**	**0**	**37.69**

Table 4.8 Comparison of females' rates of aggression given and received and males' rates of grooming given by rank category (post-hoc test, Tukey's multiple-comparison of means). Significant differences between rank categories are marked in bold.

Sex	**Behaviour**	**Rank categories**	**Estimated difference**	**95%-CI**	**p-value**
FEMALES	aggression/hour (given)	2 – 1	-0.30	-2.56, 1.95	.979
		3 – 1	**-2.98**	**-5.14, -0.82**	**.006**
		4 – 1	**-3.48**	**-6.25, -0.72**	**.012**
		3 – 2	**-2.67**	**-4.13, -1.22**	**.001**
		4 – 2	**-3.18**	**-5.44, -0.92**	**.005**
		4 – 3	-0.51	-2.67, 1.65	.905
	aggression/hour (received)	2 – 1	0.78	-1.86, 3.41	.829
		3 – 1	1.52	-1.00, 4.04	.341
		4 – 1	1.78	-1.45, 5.00	.414
		3 – 2	0.74	-0.96, 2.44	.604
		4 – 2	1	-1.63, 3.63	.698
		4 – 3	0.26	-2.26, 2.78	.990
MALES	giving grooming/hour	2 – 1	0.01	-0.02, 0.03	.711
		3 – 1	0.02	-0.01, 0.04	.125
		3 – 2	0.01	-0.01, 0.03	.418

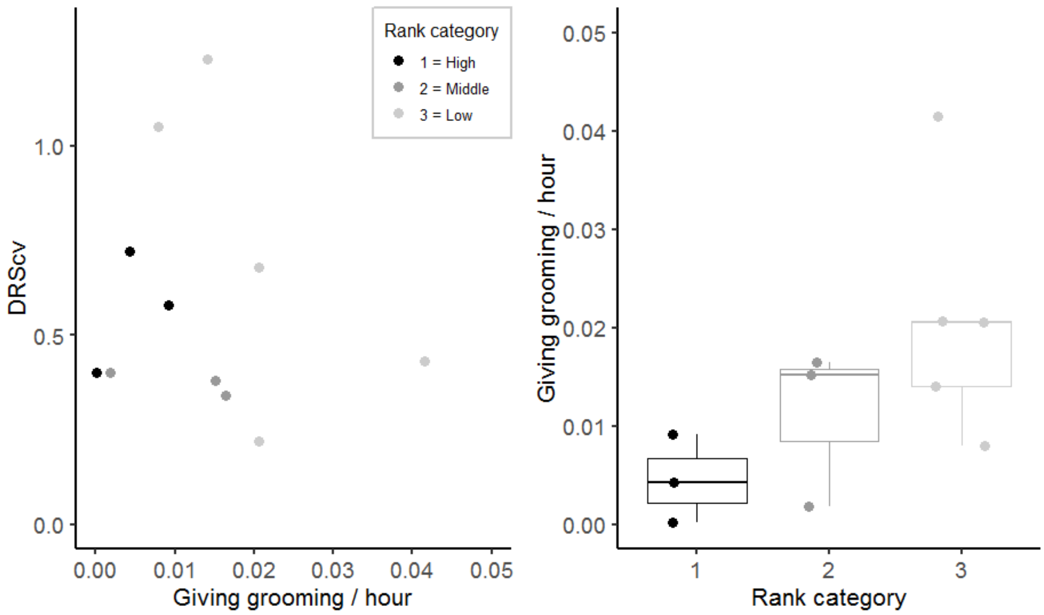


Figure 4.17 Males' DRS_{CV} in relation to rates of giving grooming [duration of grooming in hours/focal hour] on the left and males' rates of giving grooming in relation to rank category on the right (DRS_{CV}, giving grooming: Δ AIC_C = 0 and R^2 = 10.34%; giving grooming, rank: est. ± SE = 0.01 ± 0.004, p = .034).

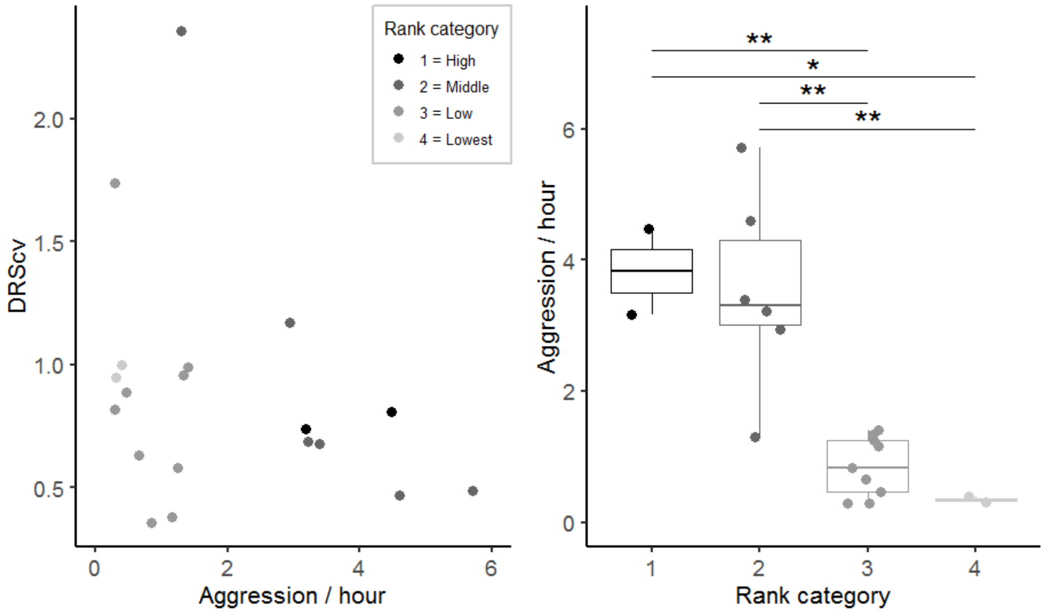


Figure 4.18 Females' DRS_{CV} in relation to rates of aggression given [count of aggression/focal hour] on the left and females' rates of aggression given in relation to rank category on the right. DRS_{CV} values were $\log_2$-transformed in analyses but raw data are presented here; asterisks indicate significance level: * $p < .05$; ** $p < .01$ (DRS_{CV}, aggression: Δ AIC_C = 0 and R^2 = 14.59%; aggression, rank: est. ± SE = -0.64 ± 0.31, p <.0001).

4.3.3 Social buffering

Hypothesis 3: Physiological stress response measures are linked to factors of sociability, reflecting social buffering.

Prediction 3i: Stronger social bonds are linked to lower mean fGCM concentrations and demonstrated reactive scope.

In female baboons, strong social bonds measured as CSI have been linked to many fitness-related measures, such as reproduction and lifespan (Silk et al., 2003; Silk et al., 2010b). While most studies have used the strength of an individual's strongest bonds, measured as the sum of the individual's three highest CSI values, others have used the number of strong or weak ties an individual maintains (McFarland et al., 2017). Here, to incorporate all these potential ways in which social bonds might link to demonstrated reactive scope or mean physiological stress response levels, models were constructed using four measures: the sum of the top three CSI values, the single highest CSI value, the number of stronger than average CSI values (i.e. CSI > 1), and the number of weaker than average CSI values (i.e. CSI < 1). These were compared to null models including age and rank category as control factors. There was a strong negative correlation between the number of strong and the number of weak bonds both for males (Pearson's product-moment correlation, $t(9) = -6.53$, $r = -0.91$, $p = .0001$, CI = -0.98, -0.68) and females (Pearson's product-moment correlation, $t(17) = -10.59$, $r = -0.93$, $p < .0001$, CI = -0.97, -0.83), as there were only a few non-bonded pairs (i.e. with a CSI of zero). Results of model comparison are presented in Table 4.9, while details of models can be found in Appendix IV-III.

As Table 4.9 shows, there was no substantial support for any of the models investigating associations between social bonds and demonstrated reactive scope measured as DRS or DRS$_{CV}$ for either males or females. There was, however, strong support for a link between social bonds and mean fGCM levels: for males, the model including the number of weak CSI values was the best model of the set with all other models having a Δ AIC$_C$ > 2, and this model explained an additional 41% of the variation in mean fGCM concentrations of males compared to the null model. Here, males with higher numbers of weak bonds had lower mean fGCM concentrations (Figure 4.19). For females, the model including the sum of the top three CSI values was the best model for mean fGCM concentrations, explaining an additional 18% of variation in mean fGCM levels compared to the null model, while all other models had a Δ AIC$_C$ > 2. Here, females with larger sums of their top three CSI values had lower mean fGCM concentrations (Figure 4.19).

LM: *stress measure ~ measure of social bonds + age class + rank category*

Table 4.9 Results of LM comparisons regarding the link between social bonds and demonstrated reactive scope (DRS and DRS$_{CV}$) and mean fGCM concentrations of males and females. Models included age and rank category; DRS and DRS$_{CV}$ values of females were log$_2$-transformed. Models with a Δ AIC$_C$ < 2 were considered to have received substantial support and are marked in bold and underlined.

	MALES						FEMALES					
	Response variable: (Δ AIC$_C$, marginal R^2 [%])											
	DRS		**DRS$_{CV}$**		**mean fGCM**		**DRS**		**DRS$_{CV}$**		**mean fGCM**	
Predictor:	**Δ AIC$_C$**	**R^2**	**Δ AIC$_C$**	**R^2**	**Δ AIC$_C$**	**R^2**	**Δ AIC$_C$**	**R^2**	**Δ AIC$_C$**	**R^2**	**Δ AIC$_C$**	**R^2**
sum (top 3 CSI)	6.94	31.91	7.26	8.50	5.92	40.35	2.99	3.60	3.47	7.88	**0**	**56.43**
highest CSI	3.52	47.22	5.72	17.48	9.03	25.19	3.71	0.48	3.68	7.01	2.88	49.91
no. strong CSI (CSI > 1)	5.65	38.01	7.29	8.28	6.46	37.89	2.74	4.66	3.67	7.04	7.14	38.59
no. weak CSI (CSI < 1)	6.86	32.30	7.16	9.12	**0**	**62.37**	3.32	2.18	3.71	6.90	7.27	37.91
null model	**0**	**32.80**	**0**	**9.11**	2.87	20.99	**0**	**0.28**	**0**	**7.11**	4.2	37.69

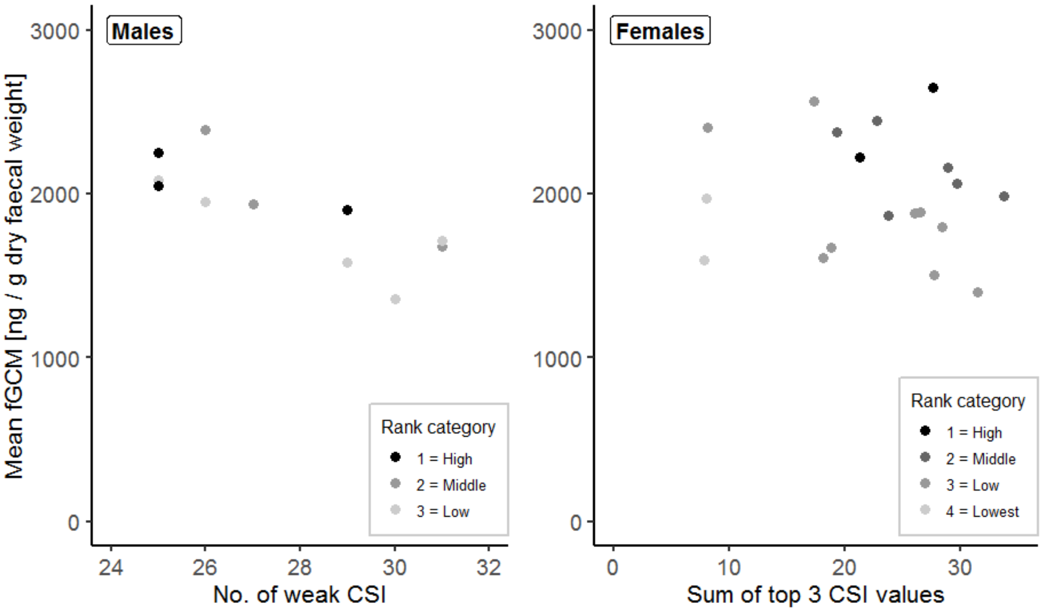


Figure 4.19 Males' mean fGCM concentrations [ng/g dry faecal weight] in relation to the number of weak CSI (i.e. CSI < 1) on the left, and females' mean fGCM concentrations in relation to the sum of their top three CSI values on the right (males, no. of weak CSI: Δ AIC$_C$ = 0 and R^2 = 62.37%; females, sum of top 3 CSI values: Δ AIC$_C$ = 0 and R^2 = 56.43%).

Prediction 3ii: Higher centrality in the affiliative social network is linked to lower mean fGCM concentrations and demonstrated reactive scope.

To investigate whether single measures of social network position in an affiliative network are linked to demonstrated reactive scope or mean fGCM concentrations, a series of models was constructed, each including one of the network metrics, and compared to each other and a null model including only age and rank category. In a second step, for full models that received substantial support based on the AIC$_C$ comparison or effect sizes, node permutation tests were conducted. Here, the attributes of the nodes were randomised 1000 times while the number of nodes stayed constant, and the models were calculated for each randomisation. This allows the comparison of the full model estimate to the randomised estimates and a calculation of a p-value based on this comparison. A p-value < .05 indicates a significantly low probability that the observed link between predictor and response variable happened by chance (Farine and

Whitehead, 2015). Overall results of model comparisons are presented in Table 4.10, with results of the permutation tests shown in Table 4.11, while details of all models and the permutation procedure are given in Appendix IV-III. The affiliative social network based on dyadic CSI values of all study subjects is shown in Figure 4.20.

For males, there was high multicollinearity between individual clustering coefficient and age for all response variables, with VIFs > 5, thus age was excluded from the respective full models. As Table 4.10 shows, there was substantial support for the full model including individual clustering coefficient being the best model explaining both DRS and mean fGCM concentrations, with the Δ $AIC_C > 20$ for all other models. While the Δ AIC_C was thus > 2 for the mean fGCM full model including betweenness centrality, its effect size was more than twice as large as the clustering coefficient model's and the model was therefore also included in the permutation tests. Regarding DRS_{CV}, there was no substantial support for any of the full models, with the null model being the best model of the set. Permutation tests showed that of the three models receiving substantial support, only the full model on mean fGCM concentrations including betweenness centrality was significantly different from randomised models. This result indicates that males with a higher betweenness centrality have higher mean fGCM concentrations (Figure 4.21).

For females, DRS and DRS_{CV} values were $\log_2$-transformed to avoid issues with model assumptions and to retain comparability with the other analyses. Here, for DRS, none of the full models received substantial support, with all Δ $AIC_C > 2$ and very small effect sizes throughout. For DRS_{CV}, however, the model including betweenness centrality received substantial support besides the null model, with a Δ $AIC_C < 2$ and an effect size about 10% larger than those of the other models. Regarding mean fGCM concentrations, the full models including strength and betweenness centrality received substantial support in addition to the null model, with the strength model having the lowest AIC_C and the other full model and the null model having a $\Delta\ \text{AIC}_C < 2$. The two full models had larger effect sizes than the null model, explaining about 47-49% of variation compared to 38% of the null model. Permutation tests revealed that the DRS_{CV} full model including betweenness centrality was not significantly different from models based on randomised networks, while the two mean fGCM full models including strength and betweenness centrality were significantly different from randomised models (Table 4.11). This indicates that for females, both strong direct affiliative connections (measured as strength) and centrality in an affiliation network (measured as betweenness centrality) are linked to lower mean fGCM concentrations (Figure 4.22), thus showing the opposite relationship between mean fGCM concentrations and betweenness centrality to that seen in males.

LM: *stress measure ~ network metric + age class + rank category*

Table 4.10 Results of LM comparisons regarding the link between position in an affiliative social network based on dyadic CSI and demonstrated reactive scope (DRS and DRS_{CV}) and mean fGCM concentrations of males and females. Models included age and rank category; DRS and DRS_{CV} values of females were $\log_2$-transformed. Models with a $\Delta\ \text{AIC}_C < 2$ or strikingly large effect sizes were considered to have received substantial support and are marked in bold and underlined.

	MALES						FEMALES					
	Response variable: ($\Delta\ \text{AIC}_C$, marginal R^2 [%])											
	DRS		**DRS_{CV}**		**mean fGCM**		**DRS**		**DRS_{CV}**		**mean fGCM**	
Predictor behaviour:	**$\Delta\ \text{AIC}_C$**	**R^2**	**$\Delta\ \text{AIC}_C$**	**R^2**	**$\Delta\ \text{AIC}_C$**	**R^2**	**$\Delta\ \text{AIC}_C$**	**R^2**	**$\Delta\ \text{AIC}_C$**	**R^2**	**$\Delta\ \text{AIC}_C$**	**R^2**
strength	29.48	32.29	7.21	8.78	28.35	39.86	3.61	0.9	3.58	7.44	**0**	**48.81**
eigenvector centrality	29.95	29.95	6.35	13.91	28.96	37.12	3.75	0.28	3.75	6.74	3.14	40.48
betweenness centrality	29.89	30.23	6.65	12.14	**21.47**	**64.88**	3.04	3.35	**0.94**	**17.79**	**0.75**	**46.92**
clustering coefficient	**0**	**32.14**	2.36	3.93	**0**	**30.3**	3.73	0.39	3.69	6.98	3.73	38.83
reach	28.85	35.33	7.3	8.23	27.83	42.18	3.7	0.51	3.57	7.49	4.34	37.06
null model	22.62	32.80	**0**	**9.11**	25.2	20.99	**0**	**0.28**	**0**	**7.11**	**0.87**	**37.69**

Table 4.11 Results of permutation tests regarding the link between network position in an affiliative network based on dyadic CSI and demonstrated reactive scope (DRS and DRS$_{CV}$) and mean fGCM concentrations of males and females. Models included age and rank category; DRS and DRS$_{CV}$ values of females were log$_2$-transformed, and a node permutation procedure was used with 1000 permutations. Permutation tests were based on results of the model comparisons in Table 4.10. Models with a $p < 0.05$ are marked in bold.

	Stress measure	**Metric**	**Proportion observed est. < randomised est.**	**Proportion observed est. > randomised est.**
MALES	DRS	clustering coefficient	0.23	0.77
	mean fGCM	**betweenness centrality**	**< 0.01**	**> 0.99**
		clustering coefficient	0.75	0.25
FEMALES	DRS$_{CV}$	betweenness centrality	0.06	0.94
	mean fGCM	**strength**	**> 0.99**	**< 0.01**
		betweenness centrality	**0.97**	**0.03**

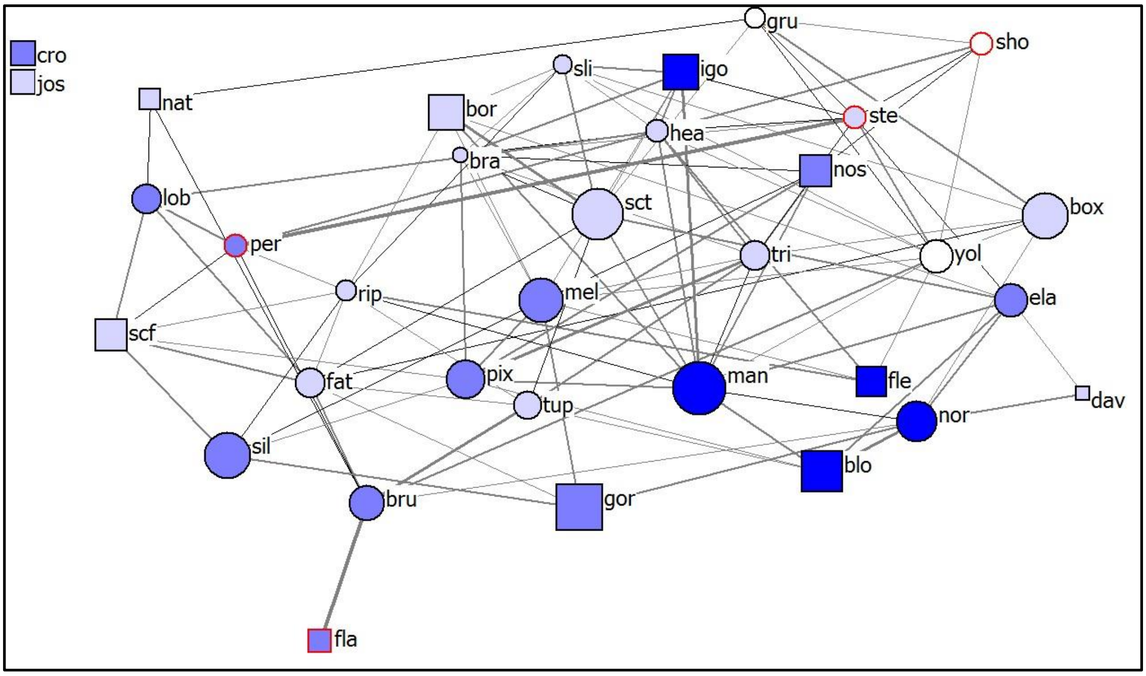


Figure 4.20 Undirected affiliative social network based on dyadic CSI values of all study subjects. Nodes represent individuals and edges represent dyadic CSI values above average (CSI > 1), with edge width reflecting bond strength. Node shape shows sex (squares = males, circles = females). Node size reflects the individuals' mean fGCM concentrations, with larger nodes symbolizing a higher mean fGCM value. Node colour represents rank category (darker = higher-ranking). Mean fGCM concentrations were not available for 4 individuals, which are marked by red rims around their nodes (fla, per, sho, ste), and which were not included in statistical models. Betweenness centrality was found to be negatively linked to mean fGCM values in females (=circles), and positively linked in males (=squares).

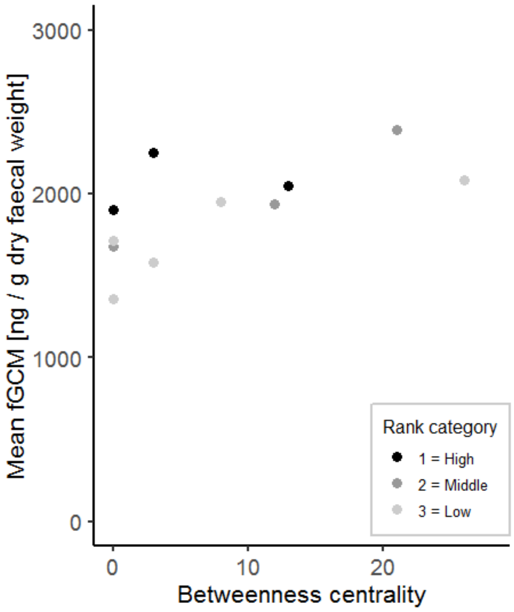


Figure 4.21 Males' mean fGCM concentrations [ng/g dry faecal weight] in relation to betweenness centrality in an affiliative social network based on dyadic CSI (Δ AIC$_C$ = 21.47 and R^2 = 64.88%, p$_{(Permutation)}$ < 0.01).

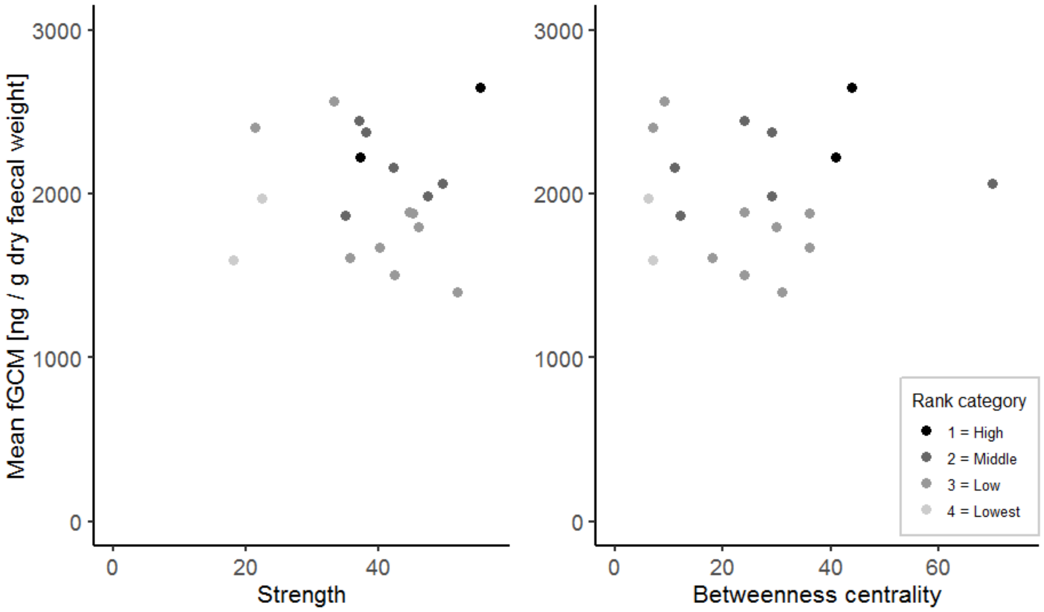


Figure 4.22 Females' mean fGCM concentrations [ng/g dry faecal weight] in relation to strength (left) and betweenness centrality (right) in an affiliative social network based on dyadic CSI (strength: Δ AIC$_C$ = 0 and R^2 = 48.81%, p$_{(Permutation)}$ < 0.01; betweenness centrality: Δ AIC$_C$ = 0.75 and R^2 = 46.92%, p$_{(Permutation)}$ = 0.03).

Prediction 3iii: Higher centrality in the agonistic social network is linked to lower mean fGCM concentrations and demonstrated reactive scope.

To investigate whether the position in agonistic networks was linked to demonstrated reactive scope or mean physiological stress response levels, a network based on all agonistic interactions between focal subjects was constructed. In addition to the metrics used for the CSI network analysis, degree was also calculated here. There was, however, high multicollinearity between degree and rank category for males, so that rank was excluded from the respective models. DRS and DRS_{CV} values of females were again log_2-transformed to comply with model assumptions. Results from the model comparisons are presented in Table 4.12 and results from node permutation tests are shown in Table 4.13. Model details as well as details on permutation results are compiled in Appendix IV-III. The agonistic social network is depicted in Figure 4.23.

For male DRS, the full model including degree was the best model based on AIC_C comparisons. Additionally, the full model including eigenvector centrality received some support, as it had the largest effect sizes with over 52% of variation explained, even though it had a Δ AIC_C of 2.84, and was therefore included in the permutation tests. Similarly, the eigenvector centrality model was the best model of the set explaining DRS_{CV} variation, with the degree model receiving also substantial support based on AIC_C comparison, even though it had a relatively small effect size. For mean fGCM variation, only the degree full model received substantial support, with it having the lowest AIC_C. In all cases, the null models also received substantial support. The node permutation tests showed that only the full models for DRS and DRS_{CV} including eigenvector centrality were significantly different from the random models (Table 4.13), indicating that males with higher eigenvector centrality in an agonistic network had lower demonstrated reactive scope, as shown in Figure 4.24.

Regarding females, for both DRS and DRS_{CV} the full models including degree and betweenness centrality, as well as the null models, received substantial support based on AIC_C comparisons, with the full models having effect sizes about 10% larger than the null models. For mean fGCM variation, the full model including clustering coefficient received substantial support besides the null model. Based on the permutation tests, all these full models were significantly different from random models, indicating that females with higher degree and betweenness centrality in an agonistic network had lower demonstrated reactive scope (DRS: Figure 4.25, DRS$_{CV}$: Figure 4.26), and that females with high clustering coefficient in this network had higher mean fGCM concentrations (Figure 4.27).

LM: *stress measure ~ network metric + age class + rank category*

Table 4.12 Results of LM comparisons regarding the link between position in an agonistic social network and demonstrated reactive scope (DRS and DRS$_{CV}$) and mean fGCM concentrations of males and females. Models included age and rank category; DRS and DRS$_{CV}$ values of females were log$_2$-transformed. Models with a Δ AIC$_C$ < 2 or strikingly large effect sizes were considered to have received substantial support and are marked in bold and underlined.

	MALES						FEMALES					
	Response variable: (Δ AIC$_C$, marginal R^2 [%])											
	DRS		**DRS$_{CV}$**		**mean fGCM**		**DRS**		**DRS$_{CV}$**		**mean fGCM**	
Predictor:	**Δ AIC$_C$**	**R^2**	**Δ AIC$_C$**	**R^2**	**Δ AIC$_C$**	**R^2**	**Δ AIC$_C$**	**R^2**	**Δ AIC$_C$**	**R^2**	**Δ AIC$_C$**	**R^2**
strength	3.8	48.41	2.5	41.3	7.69	19.56	3.06	5.92	3.12	9.3	3.55	36.79
degree	**0**	**36.34**	**1.49**	**9.31**	**0**	**23.91**	**0.73**	**15.22**	**0.7**	**18.69**	3.75	36.21
eigenvector centrality	**2.84**	**52.48**	**0**	**51.5**	7.81	18.94	3.52	3.96	3.05	9.60	3.34	37.42
betweenness centrality	5.73	40.75	4.62	31.36	7.77	19.16	**0**	**17.97**	**1.65**	**15.12**	3.4	37.24
clustering coefficient	7.27	33.58	7.39	16.61	7.77	19.13	4.04	1.72	3.66	7.08	**0.92**	**44.21**
reach	7.54	32.28	8.42	10.63	6.84	24.2	3.51	4.02	3.01	9.74	3.74	36.23
null model	**0.68**	**32.80**	**1.52**	**9.11**	**0.49**	**20.99**	**0.62**	**0.28**	**0**	**7.11**	**0**	**37.69**

Table 4.13 Results of permutation tests regarding the link between network position in an agonistic network and demonstrated reactive scope (DRS and DRS$_{CV}$) and mean fGCM levels of males and females. Models included age and rank; DRS and DRS$_{CV}$ values of females were log$_2$-transformed, and a node permutation procedure was used with 1000 permutations. Permutation tests were based on results of the model comparisons in Table 4.12. Models with a $p < 0.05$ are marked in bold.

	Stress measure	**Metric**	**Proportion observed est. < randomised est.**	**Proportion observed est. > randomised est.**
MALES	**DRS**	degree	0.84	0.16
		eigenvector centrality	**0.98**	**0.02**
	DRS$_{CV}$	degree	0.68	0.32
		eigenvector centrality	**> 0.99**	**< 0.01**
	mean fGCM	degree	0.10	0.90
FEMALES	**DRS**	**degree**	**> 0.99**	**< 0.01**
		betweenness centrality	**> 0.99**	**< 0.01**
	DRS$_{CV}$	**degree**	**0.99**	**0.01**
		betweenness centrality	**0.96**	**0.04**
	mean fGCM	**clustering coefficient**	**0.02**	**0.98**

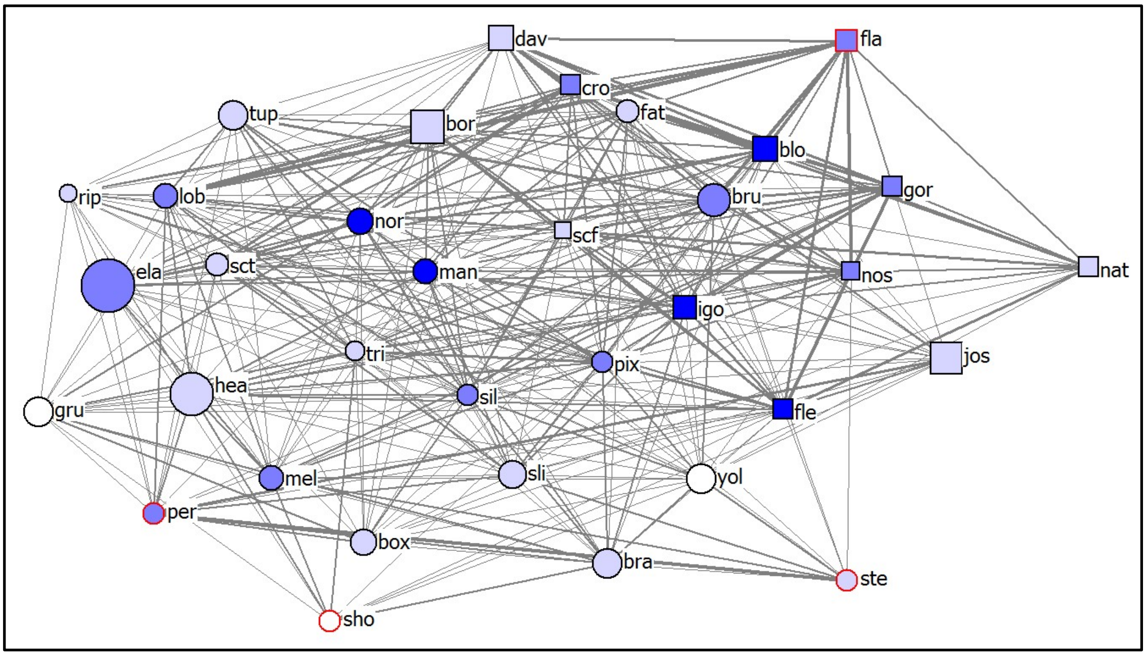


Figure 4.23 Undirected social network based on agonistic behaviour of all study subjects. Nodes represent individuals and edge widths represent the rate of any kind of agonistic (i.e. aggressive or submissive) behaviour. Node shape shows sex (squares = males, circles = females). Node size reflects the individuals' $\mathrm{DRS}_{\mathrm{CV}}$ values, with larger nodes symbolizing a higher $\mathrm{DRS}_{\mathrm{CV}}$. Node colour represents rank category (darker = higher-ranking). $\mathrm{DRS}_{\mathrm{CV}}$ values were not available for 4 individuals, which are marked by red rims around their nodes (fla, per, sho, ste), and which were not included in statistical models. For males (=squares), eigenvector centrality was negatively linked to $\mathrm{DRS}_{\mathrm{CV}}$, while for females (=circles) betweenness centrality was negatively linked to $\mathrm{DRS}_{\mathrm{CV}}$, i.e. in both sexes more central individuals had lower demonstrated reactive scope values.

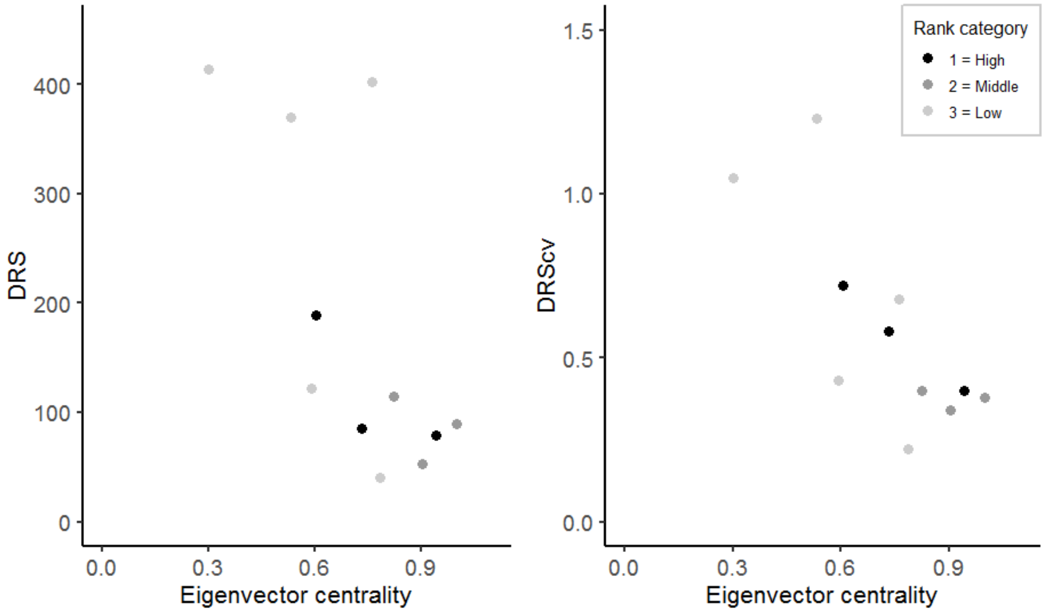


Figure 4.24 Males' demonstrated reactive scope measured as DRS (left) and $\mathrm{DRS}_{\mathrm{CV}}$ (right) in relation to eigenvector centrality in an agonistic social network (DRS, eigenvector centrality: $\Delta\ \mathrm{AIC}_{\mathrm{C}} = 2.84$ and $R^2 = 52.48\%$, $p_{(\mathrm{Permutation})} = 0.02$; $\mathrm{DRS}_{\mathrm{CV}}$, eigenvector centrality: $\Delta\ \mathrm{AIC}_{\mathrm{C}} = 0$ and $R^2 = 51.5\%$, $p_{(\mathrm{Permutation})} < 0.01$).

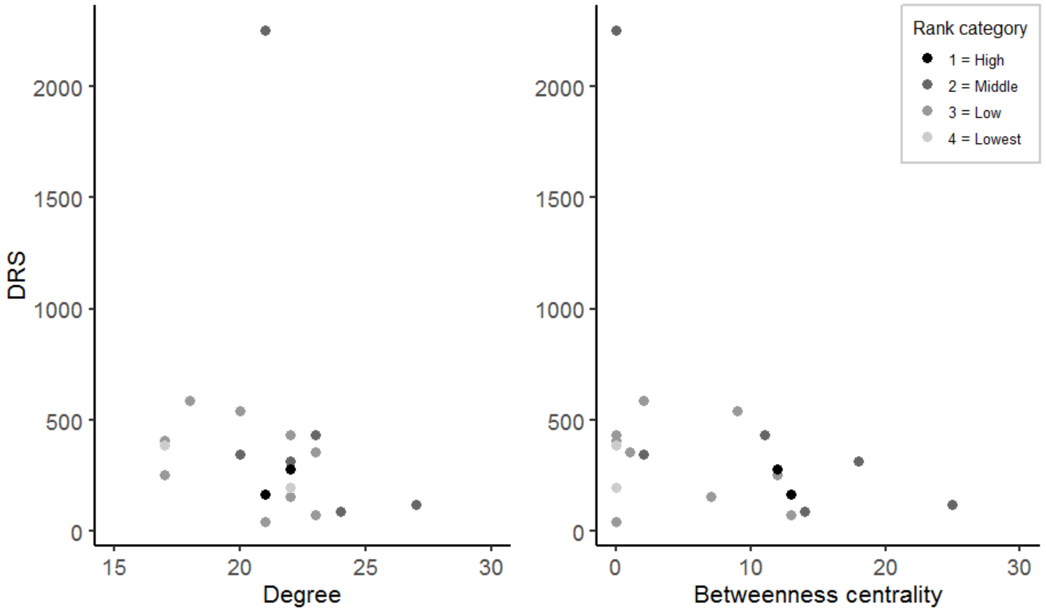


Figure 4.25 Females' demonstrated reactive scope measured as DRS in relation to degree (left) and betweenness centrality (right) in an agonistic social network. DRS values were $\log_2$-transformed in analyses, but raw data are presented here (degree: Δ $AIC_C = 0.73$ and $R^2 = 15.22\%$, $p_{(Permutation)} < 0.01$; betweenness centrality: Δ $AIC_C = 0$ and $R^2 = 17.97\%$, $p_{(Permutation)} < 0.01$).

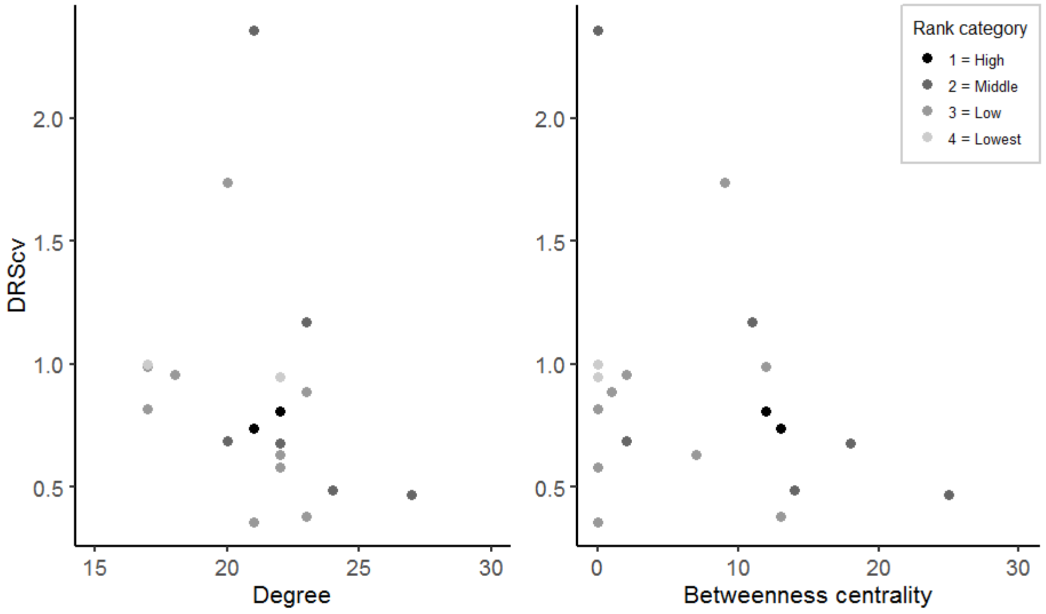


Figure 4.26 Females' demonstrated reactive scope measured as DRS_{CV} in relation to degree (left) and betweenness centrality (right) in an agonistic social network. DRS_{CV} values were $\log_2$-transformed in analyses, but raw data are presented here (degree: Δ $AIC_C = 0.7$ and $R^2 = 18.69\%$, $p_{(Permutation)} = 0.01$; betweenness centrality: Δ $AIC_C = 1.65$ and $R^2 = 15.12\%$, $p_{(Permutation)} = 0.04$).

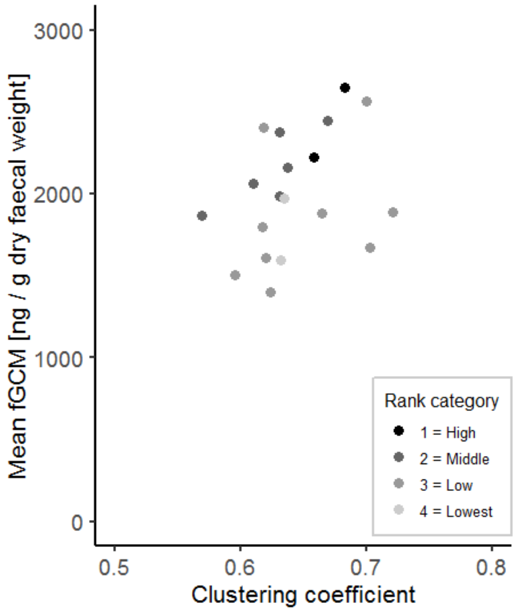


Figure 4.27 Females' mean fGCM concentrations [ng/g dry faecal weight] in relation to individual clustering coefficient in an agonistic social network (Δ AIC$_C$ = 0.92 and R^2 = 44.21%, p$_{(Permutation)}$ = 0.02).

4.3.4 Summary

In this chapter, potential coping behaviours and effects of social bonds were investigated in a comprehensive manner (for an overview of results see Table 4.14). The baboons responded with increases in scratching and total self-directed behaviour to both predation events and baiting. These changes were not directly linked to changes in fGCM concentrations. Changes in scratching in response to predation were positively linked to demonstrated reactive scope in females and negatively linked in males, but there was only weak support for a link between mean fGCM levels and scratching rates in females during baiting. Interestingly, in the longer-term, there was no link between demonstrated reactive scope or mean fGCM levels and overall rates of scratching, but for males rates of giving grooming and for females aggression rates were negatively connected to demonstrated reactive scope. Regarding social buffering, for females the strength of their strongest social bonds was associated with lower mean fGCM levels, and males with higher numbers of weak social bonds had lower mean fGCM concentrations. Using a social network approach, concordant results were found, in that in an affiliative network, females with high strength and high betweenness centrality values had lower mean fGCM levels, and males with higher betweenness centrality had higher mean fGCM concentrations. Regarding integration in an agonistic network, males with higher values of eigenvector centrality had lower demonstrated reactive scope; females with high degree and betweenness centrality in this network also had lower demonstrated reactive scope, and those with higher clustering coefficients had higher mean fGCM concentrations.

Table 4.14 Summary of the results of chapter 4, investigating whether individuals increased their rates of potential coping behaviours after aversive situations and whether changes in these behaviours were linked to changes in fGCM concentrations or longer term physiological stress response measures (mean fGCM concentrations, and DRS and DRS$_{CV}$ as measures of demonstrated reactive scope); investigating the link between overall rates of potential coping behaviours and physiological stress response measures; as well as between factors of sociability (social bonds measured via dyadic CSI, and network position in either an affiliation or agonism network) and physiological stress response measures. Findings supporting predictions are marked by a grey background; direction of changes in behaviour are described, direction of estimates of fixed effects in LMs/LMMs are indicated by ↓ for negative prediction and ↑ for positive prediction (♀ = female, ♂ = male, ns = not significant, SDB = all self-directed behaviours, SR = scratching, AG = agonism, AGGR = aggression, GR = grooming).

Hypothesis 1: Baboons use coping behaviours to manage their physiological stress response in aversive situations.			
	Self-directed behaviour	**Affiliative behaviour**	**Agonistic behaviour**
Predation:			
behaviour increases	♀ increase (SDB: p = .013) ♂ ns	♀ ns ♂ ns	♀ ns ♂ ns
change in behaviour correlated with change in fGCM	♀ ns ♂ ns	♀ ns ♂ ns	♀ ns ♂ ns
change in behaviour predicted by mean fGCM/DRS/DRS$_{CV}$	♀ DRS & DRS$_{CV}$ (SR & SDB: ↑) ♂ DRS$_{CV}$ (SR: ↓)	♀ ns ♂ ns	♀ ns ♂ ns
Baiting:			
behaviour increases	♀ increase (SDB: p = .014) ♂ increase (SDB: p = .011)	♀ ns ♂ ns	♀ increase (AG: p = .014) ♂ ns
change in behaviour correlated with change in fGCM	♀ ns ♂ ns	♀ ns ♂ ns	♀ ns ♂ ns
change in behaviour predicted by mean fGCM/DRS/DRS$_{CV}$	♀ mean fGCM (SR & SDB: ↑) ♂ ns	♀ ns ♂ ns	♀ ns ♂ ns
Hypothesis 2: Individuals use long-term coping behaviour to manage their physiological stress response measures.			
	Self-directed behaviour	**Affiliative behaviour**	**Agonistic behaviour**
Mean fGCM/DRS/DRS$_{CV}$ predicted by rates of behaviour	♀ ns ♂ ns	♀ ns ♂ DRS & DRS$_{CV}$ (GR given: ↓)	♀ DRS & DRS$_{CV}$ (AGGR: ↓) ♂ ns
Hypothesis 3: Physiological stress response measures are linked to factors of sociability, reflecting social buffering.			
	Mean fGCM	**DRS**	**DRS$_{CV}$**
Mean fGCM/DRS/DRS$_{CV}$ predicted by			
social bonds	♀ strength of strong b. ↓ ♂ no. of weak bonds ↓	♀ ns ♂ ns	♀ ns ♂ ns
centrality in affiliation network	♀ strength & betweenness centr. ↓ ♂ betweenness centr. ↑	♀ ns ♂ ns	♀ ns ♂ ns
centrality in agonism network	♀ clustering coefficient ↑ ♂ ns	♀ degree & betweenness centr. ↓ ♂ eigenvector centr. ↓	♀ degree & betweenness centr. ↓ ♂ eigenvector centr. ↓

4.4 Discussion

The aim of this chapter was to investigate coping behaviour in chacma baboons in a comprehensive manner, by looking both at short-term changes in behaviour and their potential link to physiological stress response measures, as well as at the link between long-term behavioural rates and social bonds, and physiological stress response measures. I found evidence that chacma baboons used scratching as a coping behaviour, even though this was not linked to physiological stress response measures consistently. In the long-term, there was evidence that females used aggression, while males used affiliation, to manage their physiological stress responses, but only in females were social bonds connected to lower mean physiological stress response levels, potentially reflecting social buffering.

4.4.1 Coping behaviour

Hypothesis 1: Baboons use coping behaviours to manage their physiological stress response in aversive situations.

Hypothesis 1.1: Individuals use behavioural responses to cope with aversive situations.

Prediction 1.1i: Rates of self-directed/affiliative/agonistic behaviour increase after a predation event compared to baseline levels.

While many inherent factors influence how well individuals cope with everyday stressors, animals might also use coping behaviours to reduce potential negative effects of heightened physiological stress response levels (Wechsler, 1995). It was predicted that baboons would increase their rates of self-directed, affiliative, or agonistic behaviour in response to each of two predation events to help them cope with these stressors. Behavioural rates did not significantly change for either sex after the first predation event. Females increased their rates of scratching and of all self-directed behaviours after the second predation event, however, whereas there was no significant increase in any of the three behaviours for males. While these results might be indicating that there was a difference between the two predation events, it is important to consider that the different findings may be due to a smaller behavioural sample size after the first predation event (14.5 hrs pre- and 8.4 hrs post-predation 1 vs 31.3 hrs pre- and 13.8 hr post-predation 2), as rates of scratching and other self-directed behaviours increased for both predator attacks.

Generally, the observed increase in self-directed behaviour of females is in accordance with previous findings on short-term coping behaviour in non-human primates. Gustison et al. (2012), for example, observed that female Barbary macaques (*Macaca sylvanus*) increased their scratching rates in the 5 minutes following a mild, experimental stressor. It is interesting to note, that using such a mild stressor, Gustison et al. (2012) only found an increase in scratching in the subsequent 5, but not 20 minutes. Here, due to the observational nature of the study, no such quick observations could be made so no data on the behaviour immediately after the attack are available. Instead, increased scratching rates were observed in females in the one and a half days following the predation, as such representing a more profound change in behaviour in response to the attack. Furthermore, the playback of a threat grunt used by Gustison et al. (2012) has a very different level of severity as a stressor compared to predation: while the threat grunt might have caused some form of anxiety or arousal and with it a short increase in scratching (and aggression), this might be more comparable to the anxiety-inducing proximity of a dominant individual, whereas a predator attack is a threat to the lives of all troop members and has profound consequences for the relatives or bonded individuals of the killed individual. Engh et al. (2006a), for example, found that female chacma baboons (*Papio ursinus*) increased their grooming effort in the month after losing a close relative to predation. Due to the limited number of predation events in the current study, it was not possible to distinguish between females who did or did not lose a bonded partner, and this might be the reason no overall change in affiliative behaviour was found. Alternatively, effects of losing a grooming partner on affiliative behaviour might be experienced more in the longer term, and therefore no change in short-term affiliative behavioural rates was observed. Gustison et al. (2012) also observed an increase in aggressive behaviour after the experimental stressor. This was not found in the chacma baboon females, so this might represent a difference between species or be linked again to the difference in stressor characteristics or timing of observations.

It is also very interesting that there was no significant increase in scratching of males in response to predation, even though rates generally increased as well. This could be interpreted as males not being as affected by the predation as females were, especially as it was a male that was killed in the second predator attack and no strong male-male bonds or coalitions were observed in the study troop. Nevertheless, one would expect an increase in stress and anxiety in males as well, considering that predator attacks also present a severe threat for their infants and males of the study troop had strong social bonds with females, as will be discussed in more detail in chapter 6. However, it has been described before that males, more so than females, will often aggressively defend their troop and attack a predator, sometimes even leading to the death of a leopard (Cowlishaw, 1994). This, in itself, might already represent males' main and successful coping behaviour: as Wechsler (1995) stated, coping behaviour aims to remove the aversive stimulus and, especially if it is not removeable, is used to mitigate the negative physiological consequences of the stressor. In the case of a predator attack, aggression towards the predator may be the most effective form of coping behaviour possible, and in each event the baboons were successful in at least temporarily deterring the leopard. Simultaneously, fighting the predator might also mean that the energy mobilised by the HPA-axis activation is immediately utilised and as such the individual might not experience prolonged physiological stress as it would if it would not show aggression towards the predator. In contrast, females might not be as involved in predator mobbing, as they are of smaller body size and many of them carried infants. This would suggest that while males show successful, aggressive coping behaviour directed at the predator, females experience a slightly longer physiological stress response and therefore show scratching as a 'displacement' coping behaviour, in that it is a behaviour not directed towards the stressor itself.

Prediction 1.1ii: Rates of self-directed/affiliative/agonistic behaviour increase during a baiting period compared to baseline levels.

The baiting period, in preparation for catching and collaring an individual, was assumed to be a prolonged stressful time for the troop members due to the high rates of aggression observed at the bait site. It was predicted that, as a result, the baboons would show increases in self-directed, affiliative, or agonistic behaviour in response to the baiting once they had left the bait site. Here, both sexes showed significant increases in rates of scratching and total self-directed behaviour. Furthermore, females significantly increased their rates of agonistic interactions. There was no change in affiliative behaviour during this period, or in aggression *per se*.

The increase in self-directed behaviour during the baiting period is in line with the results of heightened levels of scratching and self-directed behaviour in response to predation events described above, fitting the idea of scratching as a coping behaviour. In contrast to the previous analysis, however, both males and females showed this increase, whereas after predation events only an increase in scratching of females was found. This fits with the idea described above of predator defence as a male coping behaviour: during a predator attack, males usually use aggression towards the predator as a coping behaviour, whereas females might not necessarily have this behavioural opportunity and therefore utilise scratching to mitigate their physiological stress response. In the context of baiting, males do not have a clear target for their aggression and thus show the same coping behaviour as females do, which is scratching and other self-directed behaviour.

Again, these findings are in line with the observed increase in scratching in response to a mild, experimental stressor in female Barbary macaques (*Macaca Sylvanus*; Gustison et al., 2012), but in this context the results might be even more comparable than before: baiting with its clumped food patches led to high levels of aggression at the bait site, which included many threats and displaces, but only the occasional contact aggression such as bites or chases. Thus, while baiting is likely still a more severe stressor than a mild threat grunt as was used by Gustison et al. (2012), it is probably more comparable to it than a predator attack. Furthermore, behavioural observations commenced as soon as the animals left the baiting site, so at least for some animals the immediate short-term response in behaviour was recorded.

While Gustison et al. (2012) also observed increased rates of aggression in the

Barbary macaque females, here only an increase in general agonistic interactions, but not direct aggression, was observed in females, and no change in agonism seen for males. This could mean that chacma baboons really do not use aggression as a coping behaviour, but the difference might also be related to different aggression baselines of the species, i.e. chacma baboons are potentially generally more aggressive than Barbary macaques and therefore it is less probable that increases are detected; or it might be linked to the context of semi-free ranging vs wild animals, as in the latter case troop cohesiveness might be more important than in a captive setting.

Overall, this study provides evidence that chacma baboons use short-term behavioural responses to cope with stressful experiences, and, more specifically, that they use self-directed behaviour to do so. Scratching and other self-directed behaviours have often been termed ‘displacement behaviours’ and as such are thought to represent the anxiety or conflicting motivations that animals experience. I would propose, though, that these are non-exclusive concepts: ideally, when an animal experiences stress, it uses active coping behaviour to remove the aversive stimulus (or flee to remove itself from the aversive situation). If this is not possible, then the animal does not have a target for its aggressive motivation and might therefore show displacement behaviours. In this way, displacement behaviours would be shown when the original behaviour or motivation, for example aggression, cannot be expressed and should as such be considered as functional coping behaviours in addition to reflecting arousal or anxiety. Thus, it seems reasonable that baboons would commonly use aggression towards predators or threatening conspecifics as a coping behaviour, but if neither is possible use increased rates of scratching as a short-term coping behaviour instead.

Hypothesis 1.2: Behavioural responses to stressors are linked to physiological stress response measures.

Prediction 1.2i and prediction 1.2iii: Changes in self-directed/affiliative/agonistic behaviour after a predation event or during a baiting period are negatively correlated with changes in fGCM concentration.

It was predicted that changes in behaviour in response to predation and baiting would be negatively correlated with changes in fGCM concentrations, reflecting individuals ‘successfully’ using the coping behaviour and this way mediating their physiological stress response. Alternatively, this correlation could be positive, suggesting that behavioural and physiological reactivity might be linked, or there could be no correlation, either due to successful coping by some individuals, or indicating that there is no link between short-term changes in behaviour and in fGCM concentrations. Both in the context of predation and baiting, changes in behaviour were not significantly correlated with changes in fGCM concentrations contrary to predictions.

This finding could hint either at successful coping by some individuals, or at a segregation between behavioural and physiological coping processes. As Helmreich et al. (2012) found in their study, rats that were allowed to show coping behaviour while receiving tail-shocks showed less anxiety-related behaviour afterwards, but experienced the same physiological effects of tail-shock as the animals that did not show coping behaviour. This suggests that while coping behaviour might be successful in mitigating behavioural stress responses, it might not simultaneously be successful in mitigating physiological stress responses. To investigate this segregation, future studies would be needed that include other anxiety-linked behaviours, such as vigilance.

However, the non-association might also be due to methodological issues. While rates of self-directed behaviour increased for many individuals during these periods as described above, fGCM concentrations did not significantly increase during baiting or immediately after predation. While it is plausible that baiting might not actually lead to a general stress response (due to the nutritional benefits and high predictability of it), it is possible that fGCM data around these events were not detailed enough to detect short peaks in fGCM concentrations, as data were only available for 7 individuals during baiting and 13 individuals after predation events. Considering that fGCM measurements represent cumulative concentrations, more sensitive GC measures such as uGCM concentrations (Cheney and Seyfarth, 2009) and a greater sample size might be needed to detect short peaks in GC and then link these increases to changes in behaviour.

Finally, stressful situations on the one hand, and anxiety- or arousal-inducing situations on the other hand, might have different effects on behaviour and HPA-axis activity. As Neal and Caine (2016) argue, self-directed behaviour might be shown in anxiety- or arousal-inducing situations in general, but these situations might not be stressful enough to elicit a measurable HPA-axis activation. This explanation fits the presented data and is in accordance with other studies which similarly did not find links between temporally matched fGCM concentrations and rates of self-directed behaviour (olive baboons [*Papio anubis*; Higham et al., 2009]; Barbary macaques [*Macaca sylvanus*; Edwards et al., 2013]). It would therefore be useful to repeat this kind of investigation in a setting that allows much more frequent fGCM or uGCM sample collection around potentially stressful events.

Prediction 1.2ii and prediction 1.2iv: Changes in self-directed/affiliative/ agonistic behaviour after a predation event or during a baiting period are negatively linked to mean fGCM concentrations and demonstrated reactive scope.

Besides a potential link of changes in behaviour to short-term changes in fGCM concentrations, it was also predicted that changes in behaviour in response to aversive situations would be negatively associated with long-term mean physiological stress response levels and measures of variation in physiological stress levels, measured as demonstrated reactive scope. While the negative association predicted would reflect 'successful' use of coping behaviours, again, a positive link could be interpreted as potentially 'unsuccessful' coping behaviour with individuals with higher physiological reactivity showing stronger behavioural responses as well, and the absence of a link could indicate that physiological and behavioural reactivity are not connected, or that some individuals 'successfully' use coping behaviours while others do not. Results varied between the sexes and between the two contexts: for males, changes in scratching after predation were negatively linked to demonstrated reactive scope, while there was no link between physiological stress response measures and changes in behaviour during the baiting period. For females, on the other hand, changes in scratching were positively linked to physiological stress response measures in contrast to predictions, and the association was with demonstrated reactive scope in the context of predation, and with mean fGCM levels in the context of baiting. As only significant increases in scratching and total self-directed behaviour rates were observed in either context, and only models linking physiological stress response measures to these behaviours received any support, I will focus in this discussion on scratching as a potential coping behaviour. It should be noted, though, that demographic factors seemed to influence how strongly animals responded with affiliative and aggressive behaviours to the aversive situations but discussing these findings here in detail would go beyond the scope of this discussion.

While the behavioural response to these situations was relatively consistent, in that if animals showed a behavioural response, it was an increase in scratching and total self-directed behaviour, the link between these behavioural changes and the individuals' physiological stress response measures was more complex. For males, demonstrated reactive scope (DRS_{CV}) as a measure of variation in physiological stress response levels was negatively linked to changes in scratching after predation; that is males with low DRS_{CV} increased their scratching more than males with high DRS_{CV}. While this could be interpreted as evidence for scratching as a 'successful' coping behaviour and would be in line with the prediction and with previous findings of a negative link between physiological stress response measures and changes in self-directed behaviour (Watson et al., 1999; Pico-Alfonso et al., 2007), it also fits with the proposed explanation of why no consistent increase in scratching of males in response to predation was observed: if some males show aggressive behaviour towards the predator, while others do not and therefore respond with scratching, then it is possible that no general significant increase in scratching would be observed across all males. Then it is subsequently possible that males with higher demonstrated reactive scope, thought to reflect higher stress reactivity, could be the ones that show mobbing behaviour towards the predator, while males with low demonstrated reactive scope are less likely to use aggression but instead show increases in self-directed behaviour.

In contrast, females reacted more consistently with scratching to the predation events, and here a positive link to demonstrated reactive scope was found. Fitting the explanation above, females do not show as much anti-predator aggression as males do and might therefore have limited coping behaviours available. Thus, females with high demonstrated reactive scope showed stronger increases in scratching compared to females with lower demonstrated reactive scope, while males with high demonstrated reactive scope might have shown more aggression towards the predator. Unfortunately, it is not possible to test this idea conclusively with the data available, as to investigate this new hypothesis one would need to collect data on a higher number of predator attacks and do so in a more open habitat, where the behaviour of single individuals towards the predator can be observed.

Regarding behavioural responses to baiting, the findings also differ between the sexes. Even though males showed significant increases in scratching and total self-directed behaviour in this context, no clear link to any of the physiological stress response measures was found. This can be explained by the strong effect of rank category: here, higher-ranking males responded more strongly with scratching than lower-ranking males did, and this effect already explained more than 50% of the inter-individual variation in scratching increases. Thus, if stress measures did link to changes in scratching, these links were probably masked by the strong effect of rank category. Nevertheless, it is interesting that based on their dominance rank position, males respond more or less strongly with scratching to baiting, as no such difference was observed in the context of predation. I would propose, therefore, that baiting is more stressful or anxiety-inducing for higher-ranking males, probably due to the heightened rates of aggression at the bait site and the associated opportunity for younger males to try and increase their dominance rank position, as suggested by the patterns of rank change around this time (chapter 2).

For females, changes in scratching were positively associated with mean fGCM levels, but, in contrast to the predation context, not to demonstrated reactive scope. Mean fGCM levels are assumed to represent the amount of HPA-axis activation the female experiences over the study period but need to be treated carefully as baseline concentrations are unknown. Thus, it is difficult to differentiate whether females who have high mean fGCM levels were generally more ‘stressed’ during the study period or whether they have generally higher baseline concentrations. Either way, while females with high demonstrated reactive scope and thus potentially high stress reactivity were found to react more strongly to a very threatening stimulus such as predation, in the less severe context of baiting it was females with high cumulative levels of physiological stress responses who reacted more strongly. These findings suggest that, depending on the situation and the level of arousal or anxiety connected to it, animals might respond with a different intensity in their coping behaviour depending on either the strength of their stress reactivity or their cumulative levels of HPA-axis activation. The difference in the observed links depending on the stimulus might also be the reason why results differed from previous studies, which found either no link between changes in self-directed behaviour and average physiological stress response measures (Gustison et al., 2012) or found a negative association (Watson et al., 1999; Pico-Alfonso et al., 2007). Thus, future studies need to consider the intensity of the ‘stressor’ they use to investigate coping behaviour, as well as different characteristics of animals’ stress physiology. Overall, though, the findings described here are in contrast to the predicted negative link between changes in behaviour and physiological stress response measures, indicating that, at least regarding short-term coping behaviours, higher behavioural reactivity is linked to higher physiological reactivity.

In summary, this study provides evidence that chacma baboons of this troop use self-directed behaviour as coping behaviour and that changes in such behaviour are linked to long-term physiological stress response measures but found no evidence for a link to short-term changes in fGCM concentrations. There was no evidence for a link between physiological stress response measures and changes in affiliation or aggression in the situations investigated. There was, however, some indication that depending on the severity or type of stressor, individuals behaviourally responded more strongly if they had either higher mean physiological stress response levels or higher variability in their stress measures, the latter reflecting higher stress reactivity. Furthermore, it was proposed that males' (and potentially females') aggressive 'mobbing' behaviour towards the predator should be considered as a main coping behaviour in the predation context and that these individuals might therefore not show as much self-directed coping behaviour as individuals not involved in the predator defence.

4.4.2 Long-term coping behaviour

Hypothesis 2: Individuals use long-term coping behaviour to manage their physiological stress response measures.

Prediction 2i: Overall rates of self-directed/affiliative/agonistic behaviour are negatively linked to mean fGCM concentrations and demonstrated reactive scope.

If animals use coping behaviours in response to aversive situations to mediate their physiological stress responses, then long-term behavioural rates might reflect the cumulative use of coping behaviours in everyday life. Therefore, it was predicted that long-term behavioural rates would be negatively linked to physiological stress response measures, which would support the hypothesis that animals use coping behaviour to mediate their physiological stress response levels. As for the other predictions, alternatively, a positive link here might point towards a higher reactivity in both behaviour and physiological stress response measures, while no association could mean either that only some individuals successfully use coping behaviours, or that there is really no association between long-term behavioural rates and physiological stress response measures. The results of this chapter support the hypothesis that chacma baboons of the study troop use behavioural coping in the longer-term to manage their physiological stress response levels: males which showed high rates of grooming, and females that showed high rates of aggression, had lower demonstrated reactive scope (DRS_{CV}), a measure of variation in their physiological stress response levels, in line with the prediction. Both long-term coping behaviours might only be utilised by individuals of certain status, though, as low-ranking males spent significantly more time grooming than higher ranking males, and high-ranking females were more aggressive than low-ranking females. In contrast to the previously discussed predictions, overall rates of self-directed behaviour were not linked to physiological stress response measures in either sex.

Generally, it has been assumed in this study that long-term rates of coping behaviour represent the cumulative effect of short-term changes in behaviour in response to different stressors the animals experience. If they use coping behaviour to mitigate their physiological stress responses, then, overall, they should have lower variation in measured fGCM concentrations. Fittingly, males with higher rates of giving grooming and females with higher rates of aggression had lower values of the coefficient of variation of demonstrated reactive scope. This link, however, seemed to be dependent on the animal’s rank or social status, as high-ranking females were more aggressive and low-ranking males showed more grooming behaviour. This interpretation of cumulative short-term coping behaviour is corroborated by the results under prediction 1.2iv, where it was found that high-ranking females increased their aggression more strongly in response to baiting than did low-ranking females, whereas low-ranking males showed a stronger increase in grooming than did high-ranking males.

The findings for males are in line with previous studies. A study in male chacma baboons (*Papio ursinus*) found no link between average physiological stress response levels and grooming behaviour (Bergman et al., 2005), and in the current study, also no link between grooming and mean fGCM levels was found. The general availability of social support has previously been linked to lower physiological stress response measures in subordinate animals, however (Abbott et al., 2003), and grooming as a coping behaviour has been linked to lower basal and response GC concentrations in male olive baboons, even though in a reverse rank-dependent manner, i.e. high-ranking males that showed high rates of affiliation towards females within and outside of the consortship context had lower GC measures (Ray and Sapolsky, 1992). While my results indicate that here grooming might have a stress mitigating effect in lower-ranking males, this might reflect the males’ species- or troop-specific rank-dependent opportunities, as low-ranking males of the study troop might utilise grooming for example to secure mating opportunities and strengthen their non-sexual bonds, besides using it to mitigate their physiological stress responses (Sapolsky, 2005).

While for female non-human primates most studies have linked physiological stress response measures to affiliative behaviour (e.g. Barbary macaques [*Macaca sylvanus*; Shutt et al., 2007; Sonnweber et al., 2015]; chacma baboons [*Papio ursinus*;

Crockford et al., 2008; Wittig et al., 2008]), here I found no link between rates of affiliation and physiological stress response measures, but instead a negative association between rates of aggression and demonstrated reactive scope. A similar link between aggressive behaviour and basal and response GC concentrations has been described before in low-ranking male olive baboons (*Papio anubis*; Virgin and Sapolsky, 1997), but to my knowledge no study has yet shown such an association in female baboons. As for males, rates of behaviour differed between rank categories, with high-ranking females showing significantly more aggressive behaviour than low-ranking females. Based on this it seems likely that aggression as a successful coping behaviour might predominantly be available to females of a certain social status, and it would therefore be interesting to investigate further whether females of lower status utilise different coping strategies.

In summary, the findings of this study support the hypothesis that chacma baboons of the study troop use coping behaviour in the longer term to mediate their stress reactivity, measured as demonstrated reactive scope. While males used affiliative behaviour, females' aggression rates were linked to lower stress reactivity. As low-ranking males showed more affiliative, and high-ranking females more aggressive behaviour than animals of other rank positions, future research with larger sample sizes is needed to investigate how individuals use coping behaviour depending on their specific social status and the behavioural opportunities that are connected to it.

4.4.3 Social buffering

Hypothesis 3: Physiological stress response measures are linked to factors of sociability, reflecting social buffering.

Prediction 3i: Stronger social bonds are linked to lower mean fGCM concentrations and demonstrated reactive scope.

Based on the concept of social buffering, it was predicted that strong social bonds would be connected to lower physiological stress response measures, i.e. either mean fGCM concentrations or demonstrated reactive scope, in the study animals. Indeed, social bonds were linked to mean physiological stress response levels in a sex-dependent manner: while females with stronger strongest bonds had lower mean fGCM concentrations, males with a higher number of weak ties had lower mean fGCM levels.

While most coping behaviours discussed so far were linked to demonstrated reactive scope as a measure of stress reactivity, social bonds were connected to the individuals' mean physiological stress response levels. This fits the main-effect hypothesis of social bonds which has previously been investigated in chimpanzees (*Pan troglodytes schweinfurthii*): Wittig et al. (2016) found that the presence of a bonded partner was connected with lower uGCM concentrations at the time, both in aversive and affiliative as well as neutral situations. They suggest, therefore, that in non-human primates, daily engagement with bonded partners mediates the HPA-axis regulation, and that social buffering is thus not only experienced in stressful situations. The results of this current study corroborate these findings, as female baboons did not increase their affiliative behaviour after experiencing a major stressor, but instead those females with very strong bonds appeared to experience lower mean physiological stress response levels in the longer term. While Wittig et al. (2016) looked at the short-term effect the presence of a bonded individual had on uGCM levels and this current study looked at the effect of having strongly bonded partners more generally, it can be argued that these reflect the same general finding: while high CSI values are interpreted as reflecting 'strong bonds' between individuals, they are in the first place reflective of the two partners spending a lot of time together, whether it is by grooming each other, being in body contact or by being in close physical proximity. Being in close proximity to a bonded individual (with the bond being assessed by them frequently being in close proximity) was shown to be linked to lower uGCM levels across contexts in chimpanzees (Wittig et al., 2016); so, if individuals spend a large proportion of their time being in close proximity to specific partners (and thus have high CSI values), then they would have lower GC concentrations whenever they are in proximity of their bonded partners and thus also have lower overall GC concentrations, as they frequently experience the mitigating effect that being in the presence of a bonded individual has on their physiological stress response system. Therefore, I would argue that linking short-term lowered GC concentrations to the proximity of a bonded individual and linking generally lower mean GC concentrations to having strong bonds and thus frequently being in the close proximity of a preferred partner, are reflective of the same effect of social buffering.

The finding presented here is also in line with other studies in female non-human primates that also found strong social bonds to be connected to lower mean fGCM levels, e.g. in female Assamese macaques (*Macaca assamensis*; Fürtbauer et al., 2014) and rhesus macaques (*Macaca mulatta*; Brent et al., 2011), and to be linked to weaker GC increases in response to instability in female chacma baboons (*Papio ursinus*; Wittig et al., 2008). This is the first study, however, that links low mean physiological stress response levels to strong bonds in female chacma baboons.

In contrast, males' mean physiological stress response levels were not connected to the strength of their strongest bonds, but instead linked to the number of weak bonds they shared with troop members, in that males with more weak bonds had lower mean fGCM concentrations. While in chimpanzees (*Pan troglodytes schweinfurthii*) both males and females experienced lower uGCM levels when in the presence of a bonded partner (Wittig et al., 2016), chimpanzees are patrilocal (Nishida et al., 2003) and thus chimpanzee males are more likely to form strong and consistent bonds than male baboons, whose bonds to females are often of a more transient nature (Städele et al., 2019). Fittingly, males of the study troop only had between 0 and 7 strong bonds (i.e. with CSI > 1), while females had between 5 and 12 strong social bonds. In contrast to the findings described here, a study in male Barbary macaques (*Macaca sylvanus*) also found that strong social bonds between males were connected to lower GC reactivity in stressful situations (Young et al., 2014). Male Barbary macaques, however, display species-specific male-male affiliative interactions and form coalitions to secure mating opportunities (Berghänel et al., 2011), while male baboons of the study troop were not observed to form coalitions. Thus, the number of weak ties of males (i.e. with CSI < 1) might reflect the level of connectedness in the troop, where amiable relationships with a large part of the group might be linked to less conflict and more mating opportunities, and thus lower mean physiological stress response levels.

Alternatively, this finding could also indicate that males with many strong bonds have higher mean fGCM levels than males with fewer strong bonds, as the number of strong and the number of weak bonds were negatively correlated. In this case, one potential explanation would lie in the type of social bonds males form, as strong social bonds often reflect mating or parenting efforts (Städele et al., 2019). Therefore, maintaining several strong bonds to females, reflecting these efforts, might be energy demanding or more ‘stress’ inducing then reducing, which would explain generally heightened mean fGCM levels. It needs to be considered, though, that the model including the number of weak bonds and even the null model were substantially better in explaining variation in males’ mean fGCM levels than the model including the number of strong bonds, indicating that while the numbers of strong and weak bonds animals maintain are obviously linked due to the limited number of potential partners, only the number of weak bonds was, at least statistically, a good predictor of males’ mean fGCM levels. Thus, while this study provided some first evidence that the number of social bonds baboon males maintain might be linked to their mean physiological stress response levels, it will need further investigation to ascertain whether it is the presence of many weak but ‘amicable’ relationships or the lack of many strong social bonds that are linked to lower fGCM levels.

> **Prediction 3ii:** Higher centrality in the affiliative social network is linked to lower mean fGCM concentrations and demonstrated reactive scope.

Only a few studies in non-human primate species have used a social network approach to investigate the link of sociability to physiological stress response measures or fitness in general. Here, it was predicted that individuals with a higher centrality in an affiliative network would have lower mean fGCM levels or lower demonstrated reactive scope. Using a network based on dyadic CSI values (comparable to Cheney et al., 2016) and utilising a permutation approach, I found that some network measures were linked to males’ and females’ mean fGCM levels, but that the directions of the links were dependent on the sex. For males, betweenness centrality was positively related with their mean fGCM concentrations, i.e. males with high betweenness centrality also had higher mean fGCM levels. For females, however, this link was negative, as females with high betweenness centrality and a high degree of strength had lower mean fGCM levels in line with the prediction. As an undirected network was used, no functional explanations about the effect of certain behaviours, e.g. whether an individual gives or receives grooming at high frequencies, can be given – instead, centrality in this network was assumed to indicate that individuals were well-integrated into the troop by maintaining relatively strong bonds to many individuals or by having bonded partners that are well-connected themselves. More specifically, high strength in this network reflects the sum of strength of all of an individual’s social bonds, i.e. it either has many connections, or some very strong bonds, or both. High betweenness centrality on the other hand indicates that an individual connects otherwise unconnected dyads and is as such a good measure of the importance of an individual for the cohesiveness of the troop.

Regarding males, the positive link between centrality and mean physiological stress response levels fits the findings described above, where males with a high number of weak ties had lower mean fGCM levels, while the strength of bonds was not linked to their physiological stress response levels. As described above, betweenness centrality is a measure of the number of shortest paths between dyads that go through the individual in question and which connect otherwise unconnected individuals. This was calculated on a weighted network, i.e. edges were weighted based on the strength of the dyadic CSI. Therefore, individuals that have many weak ties probably do not have a high betweenness centrality, as this takes into account the edge weight to calculate shortest paths, but this was not statistically tested here. Nevertheless, males that are weakly but widely connected within the troop, as represented by a high number of weak ties, had lower mean physiological stress response levels, whereas centrality in this network appeared stress-inducing rather than alleviating. Fittingly, males with strong strongest bonds did not have lower physiological stress response levels than males with weak strongest bonds. These findings suggest that for male chacma baboons, affiliative social bonds do not mediate their physiological stress response levels, but rather that weak ties and a position on the 'periphery' of the troop are linked to lower physiological stress response levels ('periphery' here is not meant to imply a geographic position in the troop but is rather the opposite of 'centrality' in a social network, i.e. in this case, the individual does not connect many otherwise unconnected dyads and does not play a large role in cohesiveness). As described above, the finding that social bonds were not linked to low physiological stress response levels could be due to the transient nature of male-female bonds in chacma baboons, and the non-existence of male-male coalitions in the study troop, but could also be influenced by the paternal effort some males exhibited. Males that were inferred from observed mating behaviour to have sired offspring during the study period were observed to form close bonds to their suspected infants' mothers. Thus, either these strong bonds themselves, or the close proximity to additional females due to these bonds, could have led to these males being more central in an affiliative network. At the same time, exerting paternal investment and defending the mothers and infants could come with higher energetic demands and thus higher mean physiological stress response levels during the study period. To get a clearer picture of this, though, an investigation into the effects of paternal effort on males' physiological stress response measures with longer-term data would be needed.

For females, both betweenness centrality and strength were negatively linked to their mean physiological stress response levels. Strength (or ‘weighted degree’) sums the strength of ties between an individual and all its partners, while high betweenness centrality indicates that the female connects many other dyads, so these findings probably reflect the effect of strong bonds on mean physiological stress response levels: females with stronger strongest bonds are likely to also have a high degree of strength and a high betweenness centrality, as the latter measure incorporates the strength of ties between individuals when calculating shortest paths. Thus, females with strong bonds potentially also have a higher betweenness centrality as well as high strength, but this was not statistically tested in the context of this study. Therefore, it is difficult to differentiate whether strong bonds or centrality in the troop (or both) are linked to low physiological stress response levels, but either way the results support the hypothesis that female chacma baboons use social bonds to mediate their physiological stress response levels. It is important to note that the link found does not represent a causal explanation though, but rather a correlational finding, as it is also theoretically possible that females with lower physiological stress response levels are better able to form strong social bonds, but the explanation of social buffering effects here is in line with previous work.

Comparing these findings to previous studies is complex, as all studies use different methods, and most have not found a difference in mean physiological stress response levels between ranks as was described in the females of this study troop. Furthermore, no studies into the link between network position and physiological stress measures have used both males and females to incorporate within- and between-sex ties, as was done here. Instead, most studies have focused on females only. A study of female chacma baboons, for example, found that females had lower fGCM concentrations when they focused their grooming on a smaller network (Crockford et al., 2008). Furthermore, the link of GCs to social network measures seems to often be rank-dependent, as for example in female Barbary macaques (*Macaca sylvanus*) high-ranking females had lower fGCM concentrations when they had more focused grooming networks, whereas low-ranking individuals had lower fGCM levels when distributing their grooming more evenly (Sonnweber et al., 2015). Similarly, high-ranking female rhesus macaques (*Macaca mulatta*) tended to have lower levels of GCs when they had a smaller grooming network, measured as reach (Brent et al., 2011). While some of these results are comparable to the effect of strong social bonds and centrality in this study, all of them conducted intra-individual comparisons which were not possible with the sample size available here. Additionally, there was no evidence in my study for a difference between rank categories in the individuals' link between social network position and physiological stress response measures.

When looking at more general findings regarding fitness benefits of social network position, the results described in this study fit with previous findings. While it was found that in male Barbary macaques (*Macaca sylvanus*) GC reactivity was attenuated when the individuals had strong social bonds to other males (Young et al., 2014), a study of male and female Barbary macaques found that a high number of social bonds, but not bond quality, predicted lower mortality when faced with extreme weather conditions (McFarland and Majolo, 2013) with this effect potentially mediated via social huddling (Campbell et al., 2018). The finding here that males with a high number of weak ties tended to have lower mean fGCM concentrations may shed light on one potential mechanism underpinning this relationship, even though the two species differ in the kind of male-male bonds they display. Based on the reactive scope model, heightened levels of GCs due to pathology or social stress (for example due to individuals not being widely connected as indicated by a low number of weak ties) might lead to a decrease of the threshold to homeostatic overload due to wear and tear, in which case the remaining reactive scope might eventually become too narrow to cope with extreme or sustained bad weather conditions. Subsequently, the mediator concentration might collapse into the homeostatic failure range (Romero and Wingfield, 2015) and the animal might not survive. While this is just a theoretical explanation and no GC concentrations were available from the Barbary macaques in the study by McFarland and Majolo (2013) to investigate this further, it might still provide one potential mechanism for how social bonds and social integration link to survival.

Aside from this, in female chacma baboons high CSIs were linked to high eigenvector centrality, which in turn predicted infant survival even better than bond strength itself (Cheney et al., 2016). While in my study betweenness centrality and not eigenvector centrality was linked to mean physiological stress response levels, both are measures of individuals' general centrality and connectedness in their social network and might therefore also provide insights into the potential mechanism of how social connectedness links to longevity or infant survival.

Overall, according to the reactive scope model, low average physiological stress response levels are assumed to be advantageous in a fitness context and were linked in my study to being widely but weakly connected and thus having low centrality in an affiliation network for males, and to strong bonds and high centrality for females. These associations might therefore provide one potential mechanism for the link between sociality and fitness found in primate species more broadly.

Prediction 3iii: Higher centrality in the agonistic social network is linked to lower mean fGCM concentrations and demonstrated reactive scope.

Besides affiliative network position, centrality in an agonistic network was predicted to be linked to lower physiological stress response measures, based on the finding that centrality in such a network was predictive of survival in Barbary macaques (*Macaca sylvanus*; Lehmann et al., 2015). In the current study, centrality was linked to demonstrated reactive scope in that high eigenvector centrality, a measure of how well-connected one's own partners are, was linked to lower demonstrated reactive scope (both DRS and DRS_{CV}) in males, whereas high betweenness centrality was linked to lower DRS and DRS_{CV} of females. Additionally, degree, i.e. the number of partners, was similarly related to females' demonstrated reactive scope, where a high number of agonistic interaction partners predicted lower DRS and DRS_{CV}. Furthermore, a high clustering coefficient, reflecting a high degree of cliquishness, in the agonism network was linked to higher mean fGCM levels in females.

As for the affiliation network, it is difficult to find functional or mechanistic explanations for these findings as an undirected network was used (i.e. an individual being central does not, for example, necessarily indicate that it received a lot of aggression). Instead, as before, high scores in centrality measures are thought to reflect that the individual is well-connected and, for betweenness centrality, that it connects otherwise unconnected individuals. While this might not immediately seem like a positive position to occupy in an agonism network, agonistic behaviours have previously been suggested to play an important role in stabilising social networks and constructing an individual's social niche (Barrett et al., 2012). Here, specifically, a large proportion of the agonistic interactions observed were low-level aggression, i.e. displaces or mild threats, which I would propose are not necessarily stress-inducing themselves, but rather show that relationships are clear, predictable, and uncontested. Additionally, it also needs to be considered that individuals that might utilise aggression as a coping behaviour might score highly on centrality measures as well, and that high centrality, especially high eigenvector centrality, might indicate the availability of potential coalition partners.

The latter could be one potential explanation of the findings in males. Males with high eigenvector centrality, which incorporates the connectedness of one's own partners, had lower variation in their physiological stress response measures, measured both as DRS and DRS_{CV}. The agonistic 'partners' of one's own opponent could therefore be considered as potential coalition partners, and in turn having many possible coalition partners would be linked to lower stress reactivity. However, as mentioned before, coalitions between males were not frequently observed. Also, the agonism network included both males and females, so a high centrality could also reflect high aggression towards females, but this differentiation was not further investigated here. Besides this, high centrality could also be connected to fights around dominance rank positions, even though demonstrated reactive scope was not found to differ by rank, or it could reflect a good integration into the troop with many predictable relations between individuals. Ray and Sapolsky (1992), for example, found that high-ranking male olive baboons (*Papio anubis*) which were able to distinguish between neutral/mildly threatening interactions and highly threatening interactions with other males had lower basal and response GC concentrations, indicating that certain behavioural styles, rather than rank itself, were linked to low GCs. Here, the finding that high centrality was linked to low variation in physiological stress response levels might reflect the same kind of social style, fitting the idea that highly predictable agonistic relationships might render high GC reactivity unnecessary.

For females, relations between centrality and demonstrated reactive scope were generally in the same direction as in males, but here high betweenness centrality rather than eigenvector centrality was linked to lower DRS and DRS_{CV}. This measure is more difficult to interpret in an agonistic context, as it measures shortest paths that go through the individual and which connect otherwise unconnected individuals, and was therefore suggested to indicate individuals which play an important role in connecting dyads and are thus central to their network (Lehmann et al., 2015). Generally, though, both betweenness and degree can be considered measures of centrality and were linked to lower variation in physiological stress response levels, which can be explained by the same ideas already described for males, i.e. that good integration and stable and predictable relationships might mean that individuals do not need a high stress reactivity (or that individuals with low stress reactivity are better able to form stable and predictable relationships themselves). Additionally, this link might also reflect aggression having a role as a coping behaviour. Under hypothesis 2 it was described that females of the study troop appeared to use aggression in the longer-term to mediate their stress reactivity (measured as DRS_{CV}). The finding here could reflect the same effect: while it is not possible to differentiate between aggressive and submissive behaviour in the agonistic network, high rates of aggressive behaviour would be counted as a high rate of agonism and could subsequently lead to individuals being well-connected in the agonism network. It is therefore difficult to differentiate whether high betweenness centrality and high degree in an agonism network are linked to lower demonstrated reactive scope due to more predictable and stable relationships, or due to the stress-mediating effects that aggression as a coping behaviour might have. That these network measures were linked to demonstrated reactive scope, though, and not mean fGCM levels, could suggest that it is the presence of predictable relationships that explains this effect as high predictability might render high physiological stress reactivity unnecessary, but directed aggression networks would be needed to get a clearer picture on this.

Besides a study on male chimpanzees (*Pan troglodytes schweinfurthii*) which used a social network approach to investigate fitness benefits associated with agonistic social network position and more specifically coalition formation (Gilby et al., 2013), only one study has linked agonistic networks to fitness: Lehmann et al. (2015) found that Barbary macaques (*Macaca sylvanus*) with a high number of partners in an agonism network had a higher survival probability in extreme winter weather conditions, while individuals with a high clustering coefficient had low survival probability. The findings of the current study regarding the link between agonistic network position and physiological stress response measures might provide one potential mechanism of how such a network position might link to survival and fitness. Here, females with a high number of partners had lower physiological stress reactivity, measured as demonstrated reactive scope, or in contrast, low centrality and low degree in the agonism network were linked to higher stress reactivity. As described before, based on the reactive scope model, if animals need to repeatedly utilise a large range of their physiological mediator to cope with stressors, i.e. have a high stress reactivity, then the threshold to homeostatic overload might be lowered over time due to wear and tear of the physiological system, and thus the individual’s ability to cope with subsequent extreme stressors gets diminished (Romero and Wingfield, 2015). This theoretical explanation fits the findings in the Barbary macaque group, where individuals that had fewer agonistic partners and thus lower centrality in the agonism network had lower survival probability (Lehmann et al., 2015), potentially mediated by higher stress reactivity and thus a diminished reactive homeostasis range. In this way, GC concentrations might represent one way in which sociality, for example via social buffering, predictability of social relationships, or social stress, might link to survival probabilities in extreme environmental conditions.

In summary, the results support the hypothesis that physiological stress response measures in chacma baboons are linked to sociability. While for females, strong social bonds were connected to lower mean physiological stress response levels, potentially reflecting the main-effect hypothesis of social buffering, for males a high number of weak ties was linked to lower mean physiological stress response levels, potentially representing the beneficial effect of being widely but weakly connected within the troop. Regarding the affiliative social network, results were in accordance with the findings on social bonds, in that females with a high centrality had lower mean physiological stress response levels, whereas for males, lower mean physiological stress response levels were connected to a more ‘peripheral’ position in the social network. Contrastingly, centrality in an agonistic network was connected to lower demonstrated reactive scope as a measure of stress reactivity in both sexes, potentially representing the beneficial effect of stable and predictable relationships. Interestingly, measures of the affiliative network were found to be linked to mean physiological stress response levels, whereas position in an agonistic network was linked to demonstrated reactive scope. This suggests that stable and predictable agonistic relationships mediate the need for high physiological reactivity, whereas affiliative relationships might be used to manage the individual’s physiological stress response levels, potentially via oxytocin, thus representing effects of social buffering.

4.4.4 Conclusions

This chapter provides the first evidence that chacma baboons use self-directed behaviour as a displacement coping behaviour in response to stressful or arousal-inducing situations, and that these behavioural responses might be linked to physiological stress response measures. Further studies will be needed though, that have a larger dataset on behavioural responses and that capture short-term changes in fGCM concentrations in response to aversive situations, to fully investigate how physiological stress responses are linked to behavioural responses. Evidence was also provided that males use affiliative and females use aggressive behaviour to manage their physiological stress response levels. This area of enquiry could benefit from studies investigating how these coping behaviours are linked to the social or demographic status of individuals, and the behavioural opportunities or constraints they experience. Finally, this chapter describes first evidence for the main-effect hypothesis of social buffering in female chacma baboons, in that females’ strong social bonds appeared to mediate their mean physiological stress response levels, while this was not the case for males. Instead, results indicated that predictability of relations and general integration into the troop might be linked to lower physiological stress response measures in males, an area which has not received much interest in recent years. Finally, I found evidence that strong and stable agonistic relationships are beneficial for both sexes, which I would suggest is due to the higher predictability of social interactions. Overall, this study produced new knowledge regarding a potential link between sociality and fitness. In the final chapter, I will investigate potential measures of resilience, and how these link to the effects described here of coping behaviours, social buffering, and social integration.

5. Resilience in chacma baboons

5.1 Introduction

5.1.1 Concepts

In the context of this study, I have used the definition of resilience proposed by Rutter (2012): “reduced vulnerability to environmental risk experiences, the overcoming of a stress or adversity or a relatively good outcome despite risk experiences”. As a concept, resilience is a framework used in psychological and psychiatric investigations into the extensive heterogeneity in how individuals differ in their response to stress and trauma, and it has become popular in the exploration of factors that can enhance resilience in humans in recent years (reviewed for example in Snijders et al., 2018). As described in chapter 1, this study was conducted based on the three-hit concept of resilience developed in humans, where genetics (hit-1) and early environments (hit-2) are thought to interact leading to modifications of the epigenome and neuroendocrine systems to prepare the individual for the environment later in life (Daskalakis et al., 2013). Depending on these modifications, individuals are more resilient or vulnerable depending on the environment they encounter later-on (hit-3), relative to their conspecifics (Daskalakis et al., 2013).

While the fourth chapter focused on coping behaviours and social buffering, the current chapter explores the subsequent step in the process of dealing with stressors, investigating differences in individual success in coping with adversity. To reiterate, the process of resilience, as understood in humans, is composed of the appraisal of a situation, the meta-cognition of the emotions connected to the first appraisal, and the choice of coping behaviour to deal with the stressor (Fletcher and Sarkar, 2013). While it is not possible to observe the appraisal or meta-cognition, if present, in wild animals, the fourth chapter did describe findings of different coping behaviours the animals used, and this current chapter will describe the success of the animals in dealing with everyday stressors, as a proxy for the overall process of resilience.

5.1.2 Resilience in animal studies

Laboratory studies

Resilience as a term is widely used in animal studies, but it has been used in very different contexts and is often not well-defined, especially in studies of wild animals. Regarding laboratory studies, for more than 50 years the effects of early-life environment on later-in-life behaviour and stress reactivity have been extensively studied in different animal models (Korosi and Baram, 2010). Additionally, bidirectional effects of genes and environment are widely investigated, where neuronal and genetic factors influence behaviour and physiology, but at the same time experiences during critical developmental periods, e.g. pre- or postnatal ones, can lead to enduring changes in the neuronal genetic programming (Korosi and Baram, 2010). These kinds of effects have been studied in a variety of species (reviewed in Daskalakis et al., 2013; in guinea pigs [*Cavia porcellus*; Sachser et al., 2013]; in rats [*Rattus norvegicus domestica*; Korosi and Baram, 2010]; in a range of non-human primate species, as reviewed in Bennett, 2008; Stevens et al., 2009; Parker and Maestripieri, 2011).

Regarding non-human primates specifically, early studies used severe stressors and found subsequent pathologies, for example in rhesus macaques (*Macaca mulatta*; Hinde and Spencer-Booth, 1971), while more recent studies have focused on moderate stressors and their link to non-pathological, inter-individual differences in behaviour, neuronal and endocrine systems. For example, squirrel monkeys (*Saimiri* spp.)

experiencing brief intermittent maternal separation around the time of weaning were found to be less anxious, to have reduced stress-induced GC responses, to have enhanced cognitive control of behaviours regarding response inhibition, and to show more exploratory behaviour (reviewed in Lyons et al., 2009). In pair-breeding common marmosets (*Callithrix jacchus*), parental deprivation of infants was found to be related to changes in their gene expression linked to GC receptors in late adolescence, thus potentially influencing resilience even at a later stage of life (Arabadzisz et al., 2010). Furthermore, peer rearing of rhesus macaque infants was linked to increases in anxiety-related and aggressive behaviours and higher stress reactivity, and early maternal separation was associated with changes in immune and metabolic functioning (Stevens et al., 2009).

Regarding resilience effects later in life, it was found in rats (*Rattus norvegicus domestica*) that chewing as a displacement behaviour during tail-shock experiments prevented the development of stress-induced anxiety-like behaviour in different behavioural tests, which the authors interpreted as the individuals being ‘behaviourally resilient’ (Helmreich et al., 2012). However, chewing and controllability of the stressor did not have a mitigating effect on the stress-induced increase of GCs or decrease of thyroid hormones, thus hinting at what the authors call a dissociation of ‘behavioural resilience’ and circulating hormone levels (Helmreich et al., 2012). In another study, mice (*Mus musculus*) exposed to chronic restraint stress were categorised as either resilient or susceptible, depending on their GC levels, i.e. resilient individuals had higher than average basal GC levels before the stress period, which decreased with chronic stress exposure; susceptible individuals, on the other hand, had lower than average basal GC concentrations, which significantly increased during chronic restraint stress

(Kim et al., 2013). Resilient animals showed also less anxiety-related behaviour in tests after experiencing chronic stress, did not lose body weight as 'susceptible' individuals did during the stress period, and had a higher stress reactivity to an acute stressor afterwards (Kim et al., 2013). Similarly, a study in cichlid fish (*Amatitlania nigrofasciata*) described stress resilience as individuals showing no behavioural response to a new stressor, after they were repeatedly exposed to net chasing experiments (Moscicki and Hurd, 2015). Moscicki and Hurd (2015) described these animals as 'becoming resilient' and suggest that resilience in this context is the same as habituation. While coping responses can lead to neuronal and endocrine changes as described previously, I would suggest that the observed change in behaviour is indeed habituation, or possibly learned helplessness, rather than resilience in the narrower sense. Using a different approach, Stafford et al. (2015) found that the occurrence of ultrasonic vocalisation in rats during intermittent swim-stress predicted resilience, which they defined as subsequently lowered levels of anxiety-like behaviour in non-water-based tests.

Non-laboratory studies

Besides laboratory studies on early- or later-in-life effects, the term resilience has been used in many other types of animal studies. For example, resilience has been used to describe farm animals' ability to cope with short-term perturbations and return to pre-adversity status in physiological measurements, so that output is maintained, and has here been proposed to be improved by facultative learning (Colditz and Hine, 2016). On the population level, the term 'ecological resilience' has been used to describe a species' or population's ability to cope with habitat loss, for example due to deforestation or forest degradation, in Bornean orangutans (*Pongo pygmaeus*; Meijaard et al., 2010) and Zanzibar red colobus populations (*Procolobus kirkii*; Nowak and Lee, 2011). ‘Reproductive resilience’ has been defined as the ability to maintain normal reproductive processes despite experiencing disturbances, as described in alpine and arctic breeding birds (white-tailed ptarmigan (*Lagopus leucura*) and willow ptarmigan (*Lagopus lagopus*); Martin and Wiebe, 2004) and grey mouse lemurs (*Microcebus murinus*; Canale et al., 2012).

Regarding wild populations of non-human primates, only early-life effects of resilience have been studied and only in a few primate populations, with differing results or interpretation of results across studies. Here, studies have mostly focused on the *predictive adaptive response* and the *developmental constraint* hypotheses. The predictive adaptive response hypothesis proposes that early environmental factors or challenges lead to adaptive phenotypic adjustments that prepare the individual for similar environmental conditions later in life (Lea et al., 2015; Berghänel et al., 2016). It is a matter of debate, though, what kind of early-life adversity should be investigated, e.g. a severe stressor like early maternal loss vs a moderate stressor such as heightened GC levels during pregnancy, and whether these predictive adaptive responses prepare the individual for a ‘matched’ external ecological environment, which would rely on stable environmental conditions from pregnancy to adulthood, or for a ‘matched’ internal somatic state (Berghänel et al., 2016). The developmental constraint hypothesis, on the other hand, proposes a simple relationship between the quality of early-life environment and adult fitness, in that individuals who experience a high quality environment early-in-life always have a fitness benefit compared to individuals who experience a low quality environment, and thus argues that experiencing early-life adversity is always costly (Lea et al., 2015). Opinions differ on whether these two hypotheses are mutually exclusive or not (Berghänel et al., 2017).

In yellow baboons (*Papio cynocephalus*), it was found that female offspring of low-ranking mothers, born during a drought, had reduced fertility during a drought-year later on, compared to females born in high-quality years or compared to females born during the same drought but with high-ranking mothers (Lea et al., 2015). Lea et al. (2015) interpreted this as evidence that early adversity, i.e. being born to low-ranking mothers during a year of low food availability, led to life-long constraints and reduced resilience to a 'matched' later environment. Similarly, studies of the same population connected early adversity at the time of birth, such as a drought, high density in the troop, low maternal rank, low social connectedness of the mother, early maternal loss or the presence of a competing younger sibling, to reduced longevity of the respective females (Tung et al., 2016), as well as to higher mortality of their offspring, interpreted as trans-generational effects of developmental constraints (Zipple et al., 2019). In contrast, Berghänel et al. (2016) showed in Assamese macaques (*Macaca assamensis*) that low food availability was linked to heightened fGCM concentrations during the first and second trimester, which in turn were linked to faster growth and larger body size of the infants, but slower development of their motor skills. They therefore proposed that developmentally constrained individuals will always be disadvantaged compared to unconstrained individuals and will therefore never out-compete them, but that the internal predictive adaptive responses help them mediate current and future energetic needs and as such make 'the best of a bad job' (Berghänel et al., 2016). While it was not possible to assess early life adversity in the context of the current study, effects of moderate and severe stressors early in life and their link to lifetime reproductive fitness are important considerations in the context of resilience. To my knowledge, no studies so far have investigated stress resilience more broadly in a wild primate population.

5.1.3 Terminology

As becomes apparent from this literature review, the term resilience has been used in many different contexts with varying degrees of clarity of meaning. Again, resilience itself was defined in this study as “reduced vulnerability to environmental risk experiences, the overcoming of a stress or adversity or a relative good outcome despite risk experiences” (Rutter, 2012), with the focus put on the latter part of the definition (“a relatively good outcome despite risk experiences“) as discussed in chapter 1. Furthermore, ‘behavioural resilience’ will be used to describe behaviourally mediated resilience, i.e. resilience that is positively linked to specific coping behaviours, whereas ‘social resilience’ will be defined as socially mediated resilience. The latter definition is in line with the concept of social buffering, where the presence of a conspecific or of strong social bonds can lead to a mitigation of HPA-axis activation during aversive situations as well as everyday life. Accordingly, one hypothesis of this study is that resilience is socially mediated, for example due to the effect of social buffering on physiological stress response levels, or due to the availability of social support. In line with the idea that resilience might be modulated by behaviour or sociability, resilience is not considered a personality trait in the context of this study, but rather as a process of dealing with adversity, where the success depends on both internal and environmental factors at the time.

5.1.4 Measures of success

As described above, resilience will be investigated here as ‘relative success’, interpreted here as individuals’ success in dealing with everyday stressors relative to the range of GC concentrations they need to employ to deal with these stressors. A measure of success in an evolutionary (i.e. fitness) context in general is life-time reproductive success, which in turn is affected by longevity and reproductive success, i.e. survival and reproduction of offspring. While neither can be directly assessed in a time-limited study like this, it is possible to measure coat condition which has often been used as an indicator of general health and well-being (Jolly, 2009), which in turn are important aspects of longevity. Therefore, different measures of coat condition will be used as 'success' measures and investigated in the context of resilience.

While it may be possible to estimate reproductive success of females, reliable data were only available for three years, which led to a low degree of variation in reproductive success between individuals. Thus, while reproductive factors were investigated in their link to resilience, they could not be used as measures of resilience themselves. It was, however, investigated whether lactation during the study period was linked to lower resilience, based on the assumption that females might need to manage an energetic trade-off between lactation and infant care and their own self-maintenance. Similarly, it was investigated whether the loss of an infant in the last three years was connected to lower resilience, as the loss itself might present as a major stressor for the females and could thus lead to reduced resilience, or as females with lower resilience might not have the ability or energetic reserves to successfully care for the infant and thus experience a higher probability of infant loss.

Similarly, health status or wound healing could not be reliably used to assess resilience under the data collection conditions. While occurrence of superficial and severe wounds as well as any kinds of infections or illnesses were recorded over the study period, the occurrence especially of infections and severe wounds was so low that it was not appropriate to do statistical testing. Nevertheless, it should be considered that sustaining severe injuries might lead to reduced resilience to subsequent challenges, and that infections and illnesses might both be a sign of low resilience, or could be a consequence of low resilience, due to the complex interplay of the hormonal and immune system. Death of study subjects themselves was not regarded as a measure of resilience, as low resilience or high vulnerability is only one of many possible causes of death in a wild population.

Coat condition

Coat condition has often been used as a proxy of health and welfare in studies of wild and captive non-human primates as it is a non-invasive, inexpensive assessment tool (Berg et al., 2009; Jolly, 2009; Borg et al., 2014; Maréchal et al., 2016). Coat condition can be influenced both by external factors, such as parasites, skin infections or weather, and internal factors (Novak and Meyer, 2009; Borg et al., 2014). The latter include age, endocrine dysfunction, nutritional deficiencies, pregnancy, immune mediated diseases or general severe illness, all of which can adversely affect coat condition (Beisner and Isbell, 2009; Berg et al., 2009; Novak and Meyer, 2009). The specific relationship between stress and hair loss in non-human primates remains unclear, however (Novak and Meyer, 2009).

A relatively small number of studies have investigated coat condition in non-human primates, and most of these have studied alopecia specifically. There are several studies which suggest that coat condition is a good indicator of well-being; for example, in Barbary macaques (*Macaca sylvanus*) exposure to tourism was linked to worse coat and body condition (Borg et al., 2014) as well as elevated fGCM levels (Maréchal et al., 2016). In Japanese macaques (*Macaca fuscata*), wild populations had less alopecia than captive or provisioned populations (Zhang, 2011). In captive female rhesus macaques (*Macaca mulatta*), pregnancy, low rank, and old age were linked to higher degrees of hair-loss (Beisner and Isbell, 2009) and similarly, in ring-tailed lemurs (*Lemur catta*), mothers' and males' coat condition were found to decline towards the end of the dry season, while the coat condition of non-mothers remained stable (Jolly, 2009). Furthermore, in captive hamadryas baboons (*Papio hamadryas*), the switch to healthier food and with it less food competition was linked to a healthier body weight and better coat condition, as well as lower parasite burden (Cabana et al., 2018). While several studies have implied that poor coat condition was linked to psychological and physiological stress, as was observed in Barbary macaques (Maréchal et al., 2016), another study in rhesus macaques found that the occurrence of alopecia was actually associated with lower baseline levels of fGCM, indicating that there was some link between hair-loss and endocrine function, but that it is not necessarily stress-related (Steinmetz et al., 2006).

Besides these general measures of well-being, birds' plumage condition and colouration have recently been investigated in the context of 'honest signalling'. Higher conspicuousness due to lighter plumage colouration was for example linked to higher corticosterone baseline and stress response levels in rock pigeons (*Columbia livia*; Angelier et al., 2018) and female tree swallows (*Tachycineta bicolor*; Taff et al., 2019), and in the tree swallows, females with brighter breasts were also less likely to abandon their nests under stressful conditions, i.e. were more resilient, while there was no difference under non-stress conditions (Taff et al., 2019). In male great-tailed grackles (*Quiscalus mexicanus*), glossiness was positively linked with tail-length, a sexually selected trait in this species (Toomey et al., 2010). These examples suggest the occurrence of 'honest signals' based on colour or glossiness; while these are not directly transferable, a good coat quality might also function as a signal of resilience in non-human primates. In male red-fronted lemurs (*Eulemur fulvus rufus*), for example, facial colouration was found to be linked to androgen levels, but did not reflect the males' dominance rank or reproductive success (Clough et al., 2009), while facial colouration of male rhesus macaques (*Macaca mulatta*) was associated with the number of sexual solicitations they received by females (Dubuc et al., 2014).

Infrared thermography

In addition to coat condition ratings conducted by observers, infrared thermography (IRT) might be a useful approach to assess coat quality. In recent years, researchers studying animals both in captivity and in the wild have been starting to use IRT as a non-invasive measure of physiological health, and reproductive and emotional state (Cilulko et al., 2013). Measurements of temperature in the nasal or eye regions (or comb and wattle for hens), for example, have been linked to emotional states, and to a certain degree to physiological stress response measures, both in domesticated species (Herborn et al., 2015; Proctor and Carder, 2015) and non-human primates, such as rhesus macaques (*Macaca mulatta*; Nakayama et al., 2005; Kuraoka and Nakamura, 2011; Ioannou et al., 2015) and chimpanzees (*Pan troglodytes*; Kano et al., 2016). The study in chimpanzees found a link between nasal temperature and both excitement behaviour and heart rate variability, but not cortisol levels, suggesting that the peripheral vasoconstriction causing the temperature drop might be mediated by the sympathetic nervous system (Kano et al., 2016).

While it might be difficult to collect such detailed IRT measures in many non-human primate species in wild populations (but see studies in chimpanzees - Dezecache et al., 2017a; Dezecache et al., 2017b), IRT can be used to measure more general differences in coat insulation quality, which might have important fitness-related consequences for individuals. More specifically, a coat that does not insulate the body well would lead to individuals losing more body heat when in the cold, and thus to an increase in energetic demands to maintain their core temperature. A non-invasive study of wild wolves (*Canis lupus*), for example, used IRT to assess the energetic costs related to mange, and found that individuals with severe hair-loss had reduced daily travel length, which might in turn impact their food consumption rates and their fitness (Cross et al., 2016). Similarly, IRT has been explored as a method to detect mange in Spanish ibex (*Capra pyrenaica*; Arenas et al., 2002) and was used to investigate areas of heat loss in mole rats (*Bathyergidae* spp.; Sumbera et al., 2007). Recently, the first study in a wild non-human primates species has employed IRT to explore the relation of temperature measures of different body parts to subcutaneous and environmental temperatures (mantled howling monkeys [*Alouatta palliat*; Thompson et al., 2017b]), but did not use it to assess coat quality. Using IRT to investigate coat insulation quality in a healthy population is therefore a new, original approach to quantitatively assessing coat condition.

Based on this previous work on coat quality, three measures of coat condition will be assessed in the context of this present study. Using monthly coat condition ratings conducted by observers, the individual's average coat condition will be calculated, thought to cumulatively represent the individual's condition, as well as their relative change in coat condition from the beginning to the end of the dry season, assumed to reflect their success in coping with this season of lower food and water availability. Additionally, infrared measures will be investigated as a potentially useful approach to quantifying coat insulation quality.

Structure of the remaining chapter

The results section of this chapter is thus divided into two parts with different aims. The first section provides a short exploration into the collected infrared measurements, the process of determining which of these measurements will be used for the subsequent calculation of resilience, as well as the calculation of resilience measures. For this, it will first be investigated how the different IRT measurements are affected by climatic variation, and how they relate to each other. Based on these findings, one original IRT measure will be chosen to be used as a quantitative assessment of coat condition. Additionally, two measures of coat condition based on observer scoring, i.e. average coat condition and relative change in coat condition as mentioned before, will be used and all three measures of coat condition will be explored regarding potential differences between individuals based on age, rank, and reproductive state. Then, resilience will be calculated as the residuals of the modelled relationship between each of the three coat condition measures and demonstrated reactive scope, i.e. the difference between the observed coat condition and the coat condition that is predicted for their demonstrated reactive scope. Three different measures of coat condition will be used to calculate resilience as firstly, these are assumed to reflect different aspects of an individual's resilience (e.g. short-term vs longer term resilience); and secondly, to assess whether the choice of 'success measure' (e.g. whether the average coat condition or the relative change in coat condition is used) affects the subsequent resilience measures or whether the proposed measures of resilience are independent of the choice of success measure. Finally, the calculated resilience measures will be graphically depicted to show the variation in resilience between individuals and it will be explored whether there are differences in resilience measures between the sexes.

In the second part, the three chosen measures of resilience will be investigated regarding their link to demographic factors (i.e. age and rank), mean physiological stress response levels, and reproduction. Additionally, it will be investigated whether resilience is mediated by certain behaviours or sociability.

5.1.5 Hypotheses and predictions

Once the exploration and determination of measures of resilience is conducted, I will investigate resilience using the following hypotheses and predictions. It needs to be kept in mind, though, that analyses here are to a large part of an exploratory nature: for example, high resilience might be linked to high rates of coping behaviours if individuals utilise these behaviours to successfully cope with adversity and thus have higher resilience, but it is also potentially possible that individuals with higher resilience do not need to use behavioural coping mechanisms, thus leading to the opposite association. Nevertheless, it will here be investigated whether resilience is behaviourally or socially mediated under the assumption that individuals who successfully use coping behaviours, and thus show high rates of coping behaviours, or who are highly sociable would have higher resilience.

Hypothesis 1: Measures of resilience are linked to demographic factors.

Prediction 1i: Resilience decreases with age.

Prediction 1ii: High-ranking individuals are more resilient than low-ranking individuals.

Hypothesis 2: Resilience is linked to reproduction and mean physiological stress response levels.

Prediction 2i: Individuals with lower resilience have higher mean fGCM concentrations.

Prediction 2ii: Females that were lactating during the study period have lower resilience, linked to energetic trade-offs.

Prediction 2iii: Females that lost an infant in the last three years have lower resilience.

Hypothesis 3: Resilience is behaviourally or socially mediated.

Prediction 3i: High resilience is linked to high rates of self-directed/affiliative/ agonistic behaviour, reflecting behavioural resilience.

Prediction 3ii: High resilience is linked to strong social bonds, reflecting social resilience.

Prediction 3iii: High resilience is linked to high centrality in the affiliation network, reflecting social resilience.

Prediction 3iv: High resilience is linked to high centrality in the agonism network, reflecting social resilience.

5.2 Methods

5.2.1 Coat condition, faecal glucocorticoid metabolite concentrations and DRS

Measures of coat condition

Coat condition was assessed using two methods, i.e. via coat condition ratings conducted by two observers, and via infrared thermography. While the first is a more commonly used method to assess coat quality, the latter represents a newly developed method that I propose can be used to assess quantitatively and objectively the quality of coat insulation. For details on the procedures used and the sample sizes for both methods, see chapter 2, section 2.2.4.

Faecal glucocorticoid metabolite concentrations and DRS

Procedures for faecal sample collection, storage, and processing are described in detail in chapter 2, section 2.2.3. Individuals' mean fGCM concentrations and demonstrated reactive scope (DRS and DRS_{CV}) were calculated based on monthly means and were only calculated for individuals for which samples from at least four months were available (n = 19 females, n = 11 males). Details of these calculations can be found in chapter 2, section 2.2.3.2.

5.2.2 Behavioural observations, rates of behaviour, and measures of sociability

All behavioural data were collected using continuous focal observations as well as *ad libitum* data collection (Altmann, 1974). Details on protocols, durations, and study subjects can be found in chapter 2, section 2.2.1 and 2.2.2. To assess the link of resilience to dominance rank positioning, position in the hierarchy was assessed using randomised Elo-ratings (Neumann et al., 2011; Sánchez-Tójar et al., 2018) based on all decided dyadic agonistic interactions from focal observations as well as *ad libitum* collected data. Males were subsequently divided into three rank categories and females into four rank categories. Details on this procedure are provided in chapter 2, section 2.2.2.2.

As described in section 2.2.2.2, from these focal observations, rates of scratching, total self-directed behaviour, giving and receiving grooming, as well as aggression and agonism were calculated and corrected for observation time. Scratching, self-directed behaviour, aggression, and agonism were calculated as counts/focal hour, whereas giving and receiving grooming were measured in hours of grooming/focal hour. These rates of behaviour have been used in chapter 4.

Besides behavioural rates, dyadic CSIs were calculated using the focal animal data, the details of which are described in chapter 2, section 2.2.2.2. For the analysis exploring the link between bond strength and resilience, the sum of an individual's three highest CSI values was used, as well as their highest CSI score, their number of weak bonds (i.e. CSIs < 1), and their number of strong bonds (i.e. CSIs > 1), comparable to the analysis conducted in chapter 4.

The analysis regarding the link between resilience and position in social networks was also conducted as for chapter 4. An undirected affiliative network based on the dyadic CSI values and an undirected agonistic network based on the rates of all dyadic agonistic interactions were constructed including both males and females. For details on the network metrics and the permutation procedure used, see chapter 2, section 2.2.2.2.

5.2.3 Health and reproduction

It was investigated whether reproductive factors were linked to resilience in females. While no reliable paternity data were available for males, for females, data on births and the survival of their infants up to one year of age were available for three years (2015-2017). Additionally, data on infant survival were included up until October 2018 which incorporates the survival up to one year of infants that were born towards the end of the study period. The idea here was that lactation would be energetically costly and thus might be linked to reduced resilience; losing an infant could be either a major stressor for the female and thus lead to decreased resilience after the loss, or it could be a sign of low resilience of the female as low resilience might mean that the female cannot appropriately care for the infant. Thus, whether the females were lactating and whether they lost an infant during the study period were used as factors (yes/no) in the model comparisons. Additionally, the number of surviving infants in the last three years was included as a factor in the lactating analysis to assess long-term links between resilience and energetically costly reproductive success.

Data were also collected on wounds and sickness behaviour *ad libitum*. While infections and illnesses might be a sign of low resilience, wounds and injuries present challenges to the individual and might be linked to subsequently lowered resilience. However, as already mentioned above, occurrence of more severe injuries and any kinds of observable infections and illnesses was low (two individuals received severe injuries, two individuals showed clear signs of infections or sickness behaviour), and it was not possible to reliably assess the process of wound healing. Therefore, it was not appropriate to do any statistical tests on the link between health and resilience.

5.2.4 Statistical analysis

Regarding the exploration of IRT, it was first analysed whether individuals differed in measured coat temperatures using ANCOVAs that included ambient temperature as an error term. t-tests were then used to assess whether measured temperatures differed between the sexes. Finally, LMMs including individual ID as random factor were compared to investigate if weather factors affected coat temperatures and whether the three coat temperature measurements were linked to each other. Based on these results, one IRT measure was chosen; this and the two coat condition measures based on observer ratings were used to calculate resilience measures.

Measures of resilience were then calculated as the residuals of LMs using a measure of coat condition as the response variable and demonstrated reactive scope (DRS or DRS_{CV}) as predictor variable, as explained in more detail in section 5.3.2.1 of this chapter. In short, three different measures of coat condition were used as these might reflect differing aspects of resilience, and it was investigated whether these were predicted by the animals' physiological stress reactivity; even if demonstrated reactive scope might not statistically predict coat condition, calculating resilience as the residuals of linear models using coat condition as response variable and demonstrated reactive scope as predictor takes into account possible variation in coat condition that is already explained by the physiological stress response system. As a basis for this calculation, it was first tested whether the three coat condition measures were correlated with each other, whether males and females differed in their coat condition measures using t-tests or Mann-Whitney U tests depending on the distribution of coat condition measurements; differences in coat condition measures between age classes were assessed using ANOVAs, and LMs constructed to investigate links between dominance rank position and coat condition measures, and LMMs to assess the link between reproductive state and coat condition ratings. Utilising a model comparison approach, it was also assessed how much of the variation in coat condition measures was explained by the individuals' demonstrated reactive scope. To test if the new measures of resilience were correlated with each other, Pearson's product-moment correlations and Spearman's rank correlations were used for males and females, respectively. While coat condition ratings were available for 32 individuals, IRT pictures were only available for 27 individuals that were well-enough habituated; taking into account the subset of individual for which physiological stress response measures were available, resilience measures based on coat condition ratings were calculated for 30 individuals (males n = 11, females n = 19) and the resilience measure based on IRT was calculated for 26 individuals (males n = 11, females n = 15).

Regarding the investigation of factors linking to resilience, ANOVAs were used to test for differences in resilience between age classes. All remaining analyses were conducted using model comparisons based on the Information Theoretic Approach (Burnham and Anderson, 2002), as described in chapter 2, section 2.3, and Δ AIC_C and effect sizes R^2 [%] are reported. Details of all models are given in Appendix V.

5.3 Results Part I: Developing a measure of resilience

5.3.1 Exploration of infrared thermography

5.3.1.1 Exploration of infrared measurements and their link to environmental factors

As described in section 5.2.1 of this chapter, three infrared measures were developed: based on a rectangular area on the side of the torso, the average coat temperature of this area was determined, as well as the delta coat temperature of this area, based on the highest and lowest temperatures measured in the rectangle. Additionally, the maximal temperature of the whole torso was determined, which was always found in the abdominal area and which was thought to reflect actual skin temperature, in contrast to the coat temperature. To investigate which infrared measurement might be best suited for the analysis of resilience, measurements were explored regarding inter-individual differences, differences between the sexes, and whether environmental factors affected temperature measurements.

Inter-individual differences

To investigate inter-individual differences, ANCOVAs were performed using temperature measurements taken from single pictures with the ambient temperature as an error term, thus investigating whether individuals differed in their means when correcting for potential effects of ambient temperature. Only individuals with at least two pictures available were included (n = 17 individuals). Individuals differed in their mean maximal abdominal skin temperature (ANCOVA, F(16,26) = 3.00, p = .006), but not in their average coat temperature (ANCOVA, F(16,28) = 1.55, p = .152). They also differed in their delta coat temperature (ANCOVA, F(16,28) = 2.62, p = .013). Data on all individuals for which IRT pictures were available, i.e. also those that had to be excluded from the analysis of inter-individual differences because only one picture was available, are shown for males in Figure 5.1 and for females in Figure 5.2 (for one female the maximal abdominal skin temperature was not available, as she was carrying her infant in the picture).

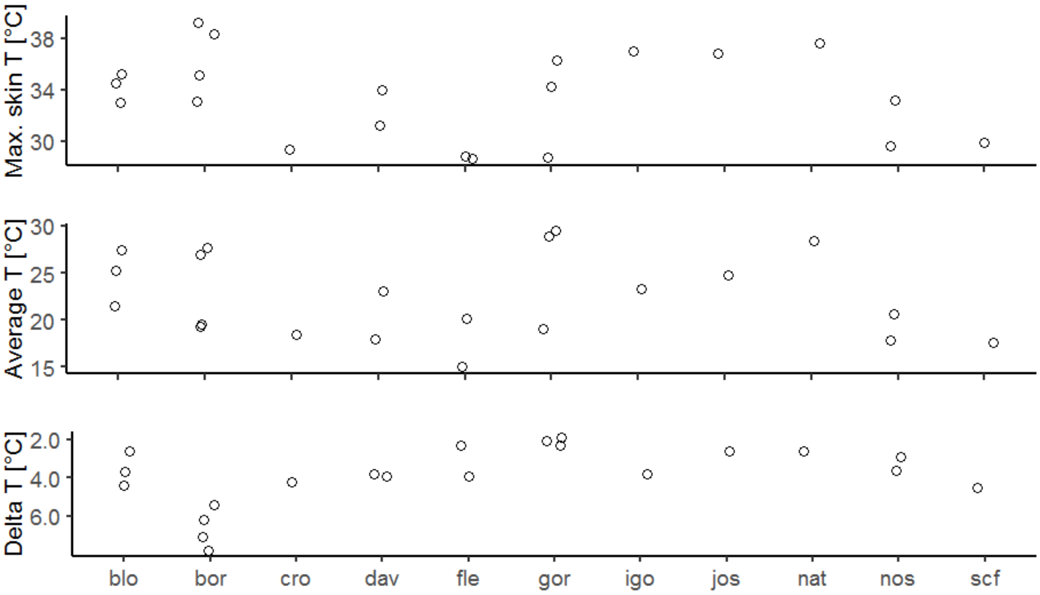


Figure 5.1 Infrared thermography measurements of males, with the maximal abdominal skin temperature [°C] shown in the top graph, the average coat temperature [°C] on the side of the animal's trunk in the middle, and the delta coat temperatures [°C] calculated from maximum and minimum coat temperatures from the side of the trunk in the bottom graph. Points reflect measurement from single pictures; individuals are sorted in alphabetical order.

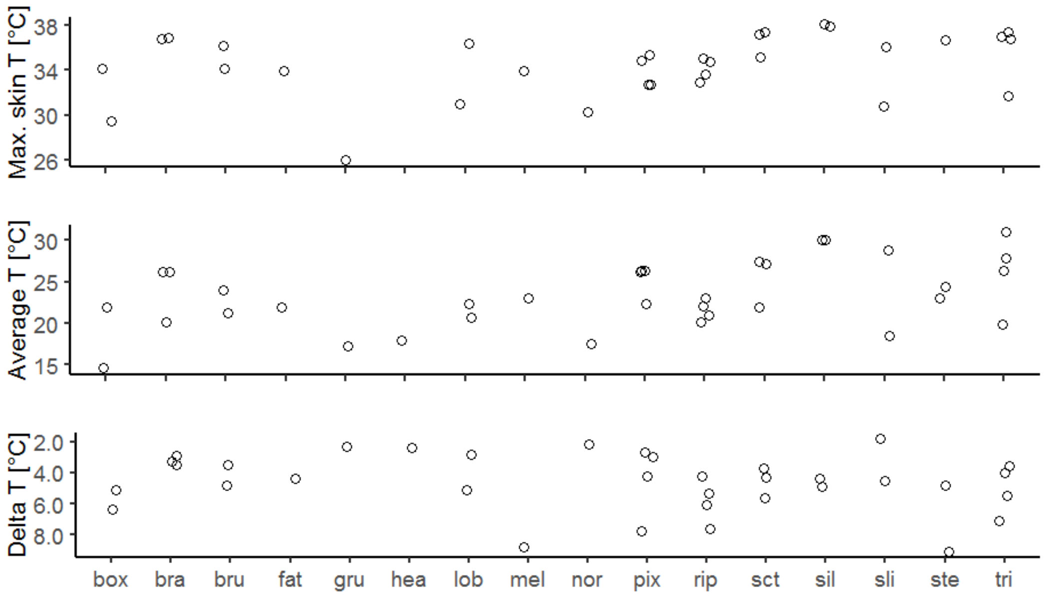


Figure 5.2 Infrared thermography measurements of females, with the maximal abdominal skin temperature [°C] shown in the top graph, the average coat temperature [°C] on the side of the animal's trunk in the middle, and the delta coat temperatures [°C] calculated from maximum and minimum coat temperatures from the side of the trunk in the bottom graph. Points reflect measurement from single pictures; individuals are sorted in alphabetical order.

Difference between the sexes

Males and females did not differ in their maximal abdominal skin temperature (t-test, t(37.23) = 1.1, p = .279, CI = -0.83, 2.79), their average coat temperature (t-test, t(38.92) = 0.78, p = .440, CI = -1.46, 3.3), or delta coat temperature (t-test, t(46.54) = 1.56, p = .125, CI = -0.21, 1.68). Therefore, all subsequent explorations of infrared measurement were done on males and females combined.

Effect of environmental factors

To investigate if environmental factors affected infrared temperature measurements, different measurements of environmental conditions were compared which could reflect apparent temperatures. Apparent temperature is the temperature an individual experiences, in contrast to the measured ambient/atmospheric temperature. Apparent temperature can for example be affected by humidity, solar radiation, and wind chill (Hill, 2006). These factors might also affect infrared measurements themselves, as humidity for example can influence how radiation travels through air, but infrared pictures were only taken in the dry season to avoid strong effects of high humidity. Therefore, models were compared including one of: ambient temperature, humidity in percent, the heat index (which combines air temperature and humidity), or the THW index (which combines temperature, humidity, and wind).

Maximal abdominal skin temperature was strongly affected by the environment, as the model including humidity was the best model of the set while no other models received any substantial support (Table 5.1). All Δ AIC_C were substantially larger than 10, and humidity explained over 70% of variation in maximal skin temperature, whereas ambient temperature and both temperature indices explained around 50%. It needs to be considered that temperature and humidity were strongly negatively correlated (Spearman’s rank correlation, $r = -0.86$, $p < .0001$), and that humidity is part of the temperature indices as well, so it is especially surprising to find such strong differences between the models. Average coat temperature was also affected by the environment, but ambient temperature and not humidity was the best predictor (Table 5.2). Here, all other models had a Δ $AIC_C > 2$, and ambient temperature explained 79% of variation in average coat temperature. In contrast to these coat measures, delta coat temperature was not predicted by any of the environmental factors investigated here, as all full models had a Δ $AIC_C > 2$ compared to the null model (Table 5.3).

LMM: *maximal abdominal skin temperature ~ environmental factor + (1|individual)*

Table 5.1 Results of LMMs regarding the effect of environmental factors on maximal abdominal skin temperatures. Models included ambient temperature, humidity [%], the Heat index, and the THW index as fixed effects, and individual ID as random factor.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	**ω**	Marginal R^2	Conditional R^2
full model:					229.06	12.55	0.002	53.6%	79.57%
Intercept	27.34	0.81	25.69, 28.94	<.0001					
ambient T	**0.33**	**0.04**	**0.26, 0.40**	**<.0001**					
full model:					216.51	0	0.997	70.7%	79.66%
Intercept	38.56	0.49	37.6, 39.53	<.0001					
humidity	**-0.10**	**0.01**	**-0.12, -0.09**	**<.0001**					
full model:					232.75	16.24	0	49.81%	78.30%
Intercept	227.36	0.85	25.61, 29.04	<.0001					
Heat index	**0.34**	**0.04**	**0.26, 0.43**	**<.0001**					
full model:					231.01	14.5	0.001	52.04%	78.42%
Intercept	27.45	0.82	25.76, 29.07	<.0001					
THW index	**0.34**	**0.04**	**0.27, 0.42**	**<.0001**					
null model:					271.21	54.7	0		42.8%
Intercept	33.88	0.54	32.77, 34.95	<.0001					

LMM: *average coat temperature ~ environmental factor + (1|individual)*

Table 5.2 Results of LMMs regarding the effect of environmental factors on average coat temperatures. Models included ambient temperature, humidity [%], the Heat index, and the THW index as fixed effects, and individual ID as random factor.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	**ω**	Marginal R^2	Conditional R^2
full model:					241.94	0	0.728	79.2%	81.48%
Intercept	12.21	0.79	10.64, 13.75	<.0001					
ambient T	**0.53**	**0.04**	**0.46, 0.61**	**<.0001**					
full model:					265.14	23.2	0	70.08%	70.32%
Intercept	28.93	0.60	27.75, 30.11	<.0001					
humidity	**-0.13**	**0.01**	**-0.16, -0.11**	**<.0001**					
full model:					246.73	4.77	0.066	77.03%	80.17%
Intercept	12.03	0.85	10.33, 13.69	<.0001					
Heat index	**0.57**	**0.04**	**0.49, 0.66**	**<.0001**					
full model:					244.46	2.52	0.206	78.38%	79.47%
Intercept	12.27	0.81	10.67, 13.84	<.0001					
THW index	**0.57**	**0.04**	**0.49, 0.64**	**<.0001**					
null model:					321.71	79.77	0		20.42%
Intercept	22.83	0.63	21.49, 24.09	<.0001					

LMM: *delta coat temperature ~ environmental factor + (1|individual)*

Table 5.3 Results of LMMs regarding the effect of environmental factors on delta coat temperatures. Models included ambient temperature, humidity [%], the Heat index, and the THW index as fixed effects, and individual ID as random factor.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2	Conditional R^2
full model:					106.41	7.97	0.018	2.44%	50.83%
Intercept	2.22	0.22	1.78, 2.65	<.0001					
ambient T	-0.01	0.01	-0.03, 0.01	.188					
full model:					109.48	11.04	0.004	2.07%	54.06%
Intercept	1.79	0.17	1.44, 2.15	<.0001					
humidity	0.003	0.002	-0.003, 0.01	.227					
full model:					106.35	7.91	0.018	2.26%	50.02%
Intercept	2.22	0.23	1.77, 2.66	<.0001					
Heat index	-0.01	0.01	-0.04, 0.01	.205					
full model:					106.44	8	0.017	2.20%	49.85%
Intercept	2.20	0.22	1.66, 2.63	<.0001					
THW index	-0.01	0.01	-0.03, 0.01	.212					
null model:					98.44	0	0.943		45.79%
Intercept	1.96	0.1	1.76, 2.15	<.0001					

5.3.1.2 Associations between infrared measurements

In addition to the exploration of how climatic variation links to infrared temperature measurements, it was also investigated if and how these measurements are linked to each other using LMMs with individual ID as random factor to account for multiple images of some individuals. Average coat temperature was strongly linked to maximal abdominal skin temperature, with a Δ AIC$_C$ of 72.91 of the null compared to the full model and the full model explaining about 69% of variation in average coat temperature (Table 5.4). Delta coat temperatures had to be log$_2$-transformed for linear models to comply with the assumptions. Delta coat temperature was not linked to maximal abdominal skin temperature, as the null model was the best model with a Δ AIC$_C$ > 2 of the full model, and the marginal R^2 of the full model only explaining 0.6% of variation (Table 5.5). The null model itself explained over 45% of variation in delta coat temperature. There was also no link between delta coat temperature and average coat temperature, as the full model had a Δ AIC$_C$ > 2 and a marginal effect size of 2% (Table 5.6).

LMM: *average coat temperature ~ maximal abdominal skin temperature*

+ (1|individual)

Table 5.4 Results of LMMs regarding the link between average coat temperatures and maximal abdominal skin temperatures. The full model included maximal skin temperature as fixed effect, and individual ID as random factor.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	**ω**	Marginal R^2	Conditional R^2
full model:					248.8	0	1	68.65%	79.02%
Intercept	-16.38	3.66	-23.65, -9.00	<.0001					
max. skin T	**1.16**	**0.11**	**0.94, 1.37**	**<.0001**					
null model:					321.71	72.91	0		20.42%
Intercept	22.83	0.63	21.49, 24.09	<.0001					

LMM: *delta coat temperature ~ maximal abdominal skin temperature + (1|individual)*

Table 5.5 Results of LMMs regarding the link between delta coat temperatures and maximal abdominal skin temperatures. The full model included maximal skin temperature as fixed effect, and individual ID as random factor.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	**ω**	Marginal R^2	Conditional R^2
full model:					102.51	4.07	0.116	0.60%	43.6%
Intercept	1.48	0.87	-0.4, 3.27	.097					
max. skin T	0.01	0.03	-0.04, 0.07	.563					
null model:					98.44	0	0.884		45.79%
Intercept	1.96	0.1	1.76, 2.15	<.0001					

LMM: *delta coat temperature ~ average coat temperature + (1|individual)*

Table 5.6 Results of LMMs regarding the link between delta coat temperatures and average coat temperatures. The full model included average coat temperature as fixed effect, and individual ID as random factor.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	**ω**	Marginal R^2	Conditional R^2
full model:					105.7	7.26	0.026	2.07%	51.51%
Intercept	2.42	0.40	1.60, 3.22	<.0001					
average coat T	-0.02	0.02	-0.05, 0.01	.233					
null model:					98.44	0	0.974		45.79%
Intercept	1.96	0.1	1.76, 2.15	<.0001					

5.3.1.3 Conclusion and choice of infrared measurement

Overall, ambient temperature was found to directly affect measured coat temperature, which can be explained as at least the outermost layer of coat will be affected by solar radiation, humidity, air temperature, and wind chill. However, I also found evidence that the coat temperature is affected by the underlying skin temperature, which in turn might reflect the individuals' thermoregulatory processes.

In the cold, for example, the animal might use vasoconstriction to diminish the blood flow to the outer layers of the skin and reduce heat loss, which would explain lower skin temperature and lower average coat temperature with low ambient temperatures. In contrast, in high ambient temperatures the individual might increase blood flow to the skin through vasodilation to increase its heat dissipation through convection or radiation. While in that case a thinner coat might theoretically be advantageous, a dense coat also protects the animal from direct solar radiation as it reflects the sunlight. Furthermore, ambient temperatures, at least when thermal pictures were taken, were never above the suggested thermal neutral zone of 25-30°C of chacma baboons (Hill, 2006), but between 10 and 29°C. Therefore, animals are not thought to have experienced heat stress or to have used thermoregulatory processes to avoid over-heating while infrared pictures were taken. Additionally, humidity was linked to temperature measurements as well, potentially due to its effects on thermoregulation, or due to its effects on the infrared measurements themselves.

Delta coat temperature was not affected by environmental factors, in contrast to maximal abdominal skin temperature and average coat temperature. It was also not linked to average coat temperature or maximal skin temperature. As there was additionally and importantly variation between individuals in their delta coat temperature, I propose using delta coat temperature as a useful quantitative IRT measurement of coat consistency, and thus coat insulation quality, and will use it as one measure of coat condition in the following assessment of resilience.

5.3.1.4 Exploration of coat condition measures

As described and explained in chapter 2, section 2.2.4, the average coat condition and the relative changes in coat condition were not correlated for either females or males. Similarly, average coat condition was not correlated with delta coat temperatures (Spearman's rank correlation, males: S = 251.79, rho = -0.14, p = .672, n = 11; females: S = 901.33, rho = -0.33, p = .219, n = 16). While the relative change in coat condition scorings was also not correlated with delta coat temperatures in females (Spearman's rank correlation, S = 571.68, rho = 0.16, p = .556, n = 16), they were significantly correlated in males (Spearman's rank correlation, S = 354.9, rho = 0.61, p = .045, n = 11), indicating that males that increased in their coat condition over the dry season also had smaller delta coat temperatures, interpreted as a more homogenous and thus a well-insulating coat, as can be seen in Figure 5.3. Measures of average coat condition, relative change in coat condition, and mean delta coat temperatures are shown for males in Figure 5.4 and for females in Figure 5.5. While it is surprising that most of these measures are not correlated with each other, this independence of coat condition measurements could indicate that they reflect different aspects of the individuals' general health and wellbeing; it also means that one needs to think carefully about what measure of coat condition should be used as a proxy for health and wellbeing in future studies, and that we should explore the use of IRT further in this context, as it might represent a more objective and precise measurement of coat quality than observer scoring.

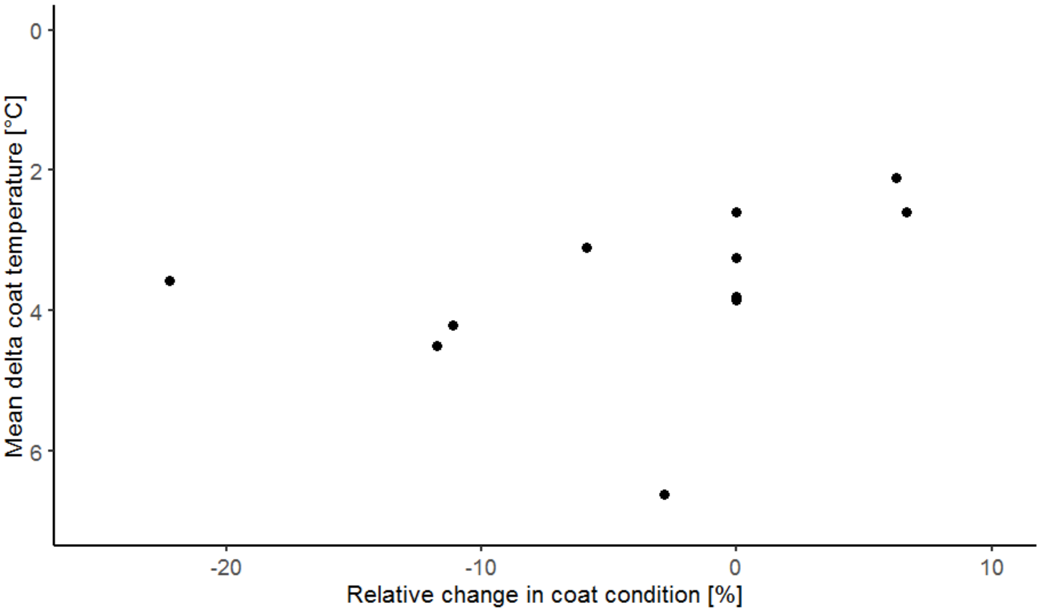


Figure 5.3 Males' mean delta coat temperature [°C] in relation to their relative change in coat condition over the dry season [%], calculated from first to last month of rating. Order of y-axis showing mean delta coat temperatures is reversed as smaller delta temperatures are assumed to be beneficial, as they reflect more homogenous coat (Spearman's rank correlation, S = 354.9, rho = 0.61, p = .045, n = 11).

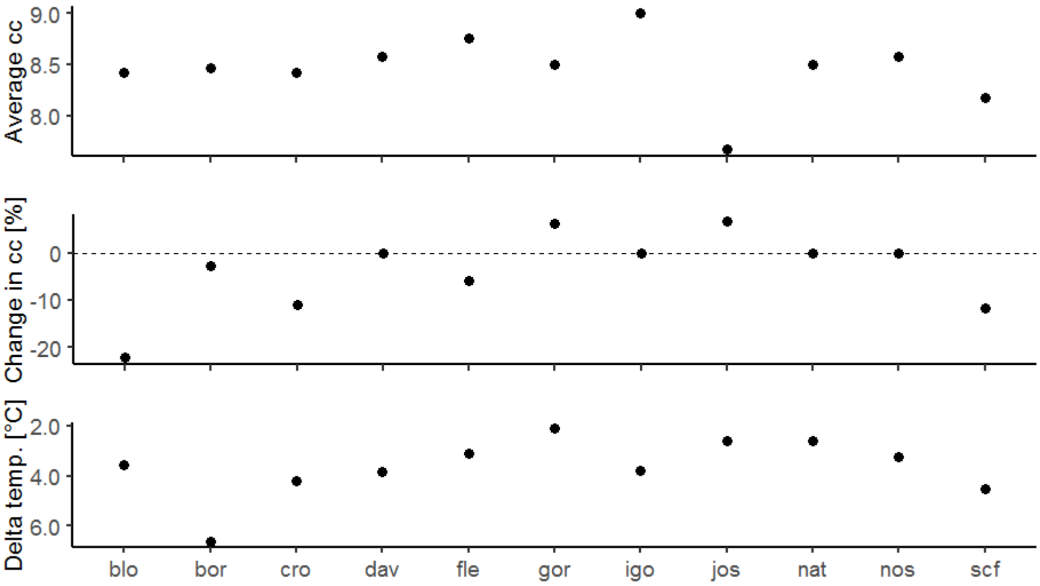


Figure 5.4 Males' coat condition measures, with the average coat condition shown in the top graph, the relative change in coat condition [%] over the dry season from first to last rating shown in the middle graph, and mean delta coat temperature [°C] in the bottom graph. Relative change could be either positive (i.e. scorings increased) or negative (i.e. scorings decreased), with the dashed line marking zero with no change. For mean delta coat temperature, small delta values were thought to reflect a more homogenous coat which would be beneficial, thus the y-axis is reversed. Individuals are marked on the x-axis in alphabetical order; n = 11.

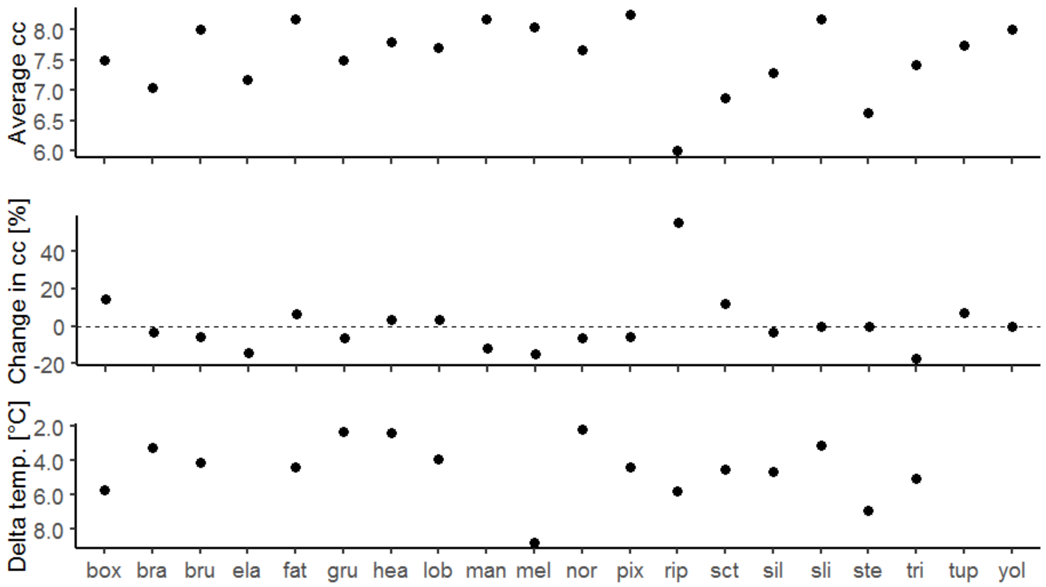


Figure 5.5 Females' coat condition measures, with the average coat condition shown in the top graph, the relative change in coat condition [%] over the dry season from first to last rating shown in the middle graph, and mean delta coat temperature [°C] in the bottom graph. Relative change could be either positive (i.e. scorings increased) or negative (i.e. scorings decreased), with the dashed line marking zero with no change. For mean delta coat temperature, small delta values were thought to reflect a more homogenous coat which would be beneficial, thus the y-axis is reversed. Individuals are marked on the x-axis in alphabetical order; n = 20 and for delta coat temperature n = 16.

For females, it was also investigated whether monthly coat condition ratings conducted by the observers were linked to the reproductive state at the time of scoring (n = 21 females). Here, model comparison showed that reproductive state at the time explained some part of the variation in coat condition ratings, with cycling females having worse coat condition than both pregnant and lactating females (Figure 5.6), indicating that carrying an infant does not necessarily lead to worse coat condition, but that females with worse health or general well-being, as indicated by worse coat condition, might be less likely to be pregnant or lactating at any given time (Table 5.7, full model details in Appendix V-I). As IRT pictures were only taken towards the end of the study period, it was not possible to investigate the link between reproductive state and IRT measurements.

LMM: *coat condition rating ~ reproductive state + age + rank + (1|individual)*

Table 5.7 Results of the LMM comparison regarding females' coat condition ratings during different reproductive states. The full model included reproductive state as a factor, and all models included age and rank category, as well as ID as random factor. Models with a Δ AICC < 2 were considered to have received substantial support and are marked in bold and underlined.

	Response variable: (Δ AIC$_C$, marginal R^2 [%])	
	coat condition	
Predictor:	**Δ AIC$_C$**	**R^2**
reproductive state	**<u>0</u>**	**<u>26.47</u>**
null model	4.66	16.45

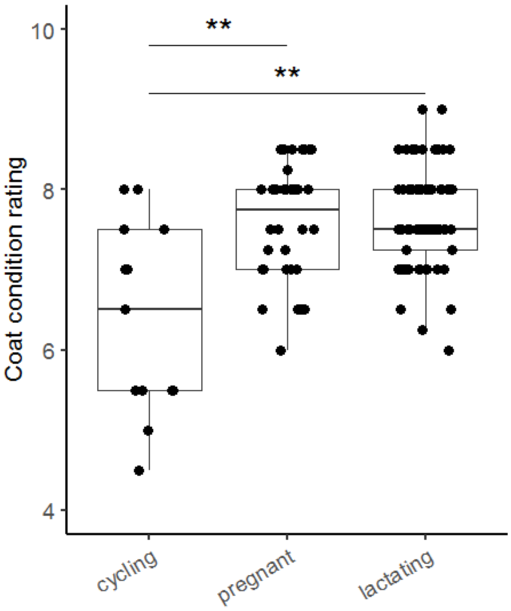


Figure 5.6 Females' coat condition ratings by their reproductive state at the time of rating (n = 21 females). In the LMM, reproductive state was a significant predictor of coat condition at the time, indicating that cycling females received significantly lower ratings than pregnant or lactating females; asterisks indicate significance level: ** p < .01.

When considering the three measures of coat condition subsequently used in the calculation of resilience, the sexes differed in their average coat condition, with males having better average coat condition than females (t-test, t(27.93) = -5.20, p < .0001, CI = -1.19, -0.52), while there were no sex differences in the relative change of coat condition (Mann-Whitney U test, W = 111, p = .795) or in delta coat temperature (t-test, t(24) = 1.16, p = .257, CI = -0.52, 1.85), as shown in Figure 5.7. To maintain comparability, because of the sex difference in one measure, all resilience measures were calculated separately for males and females.

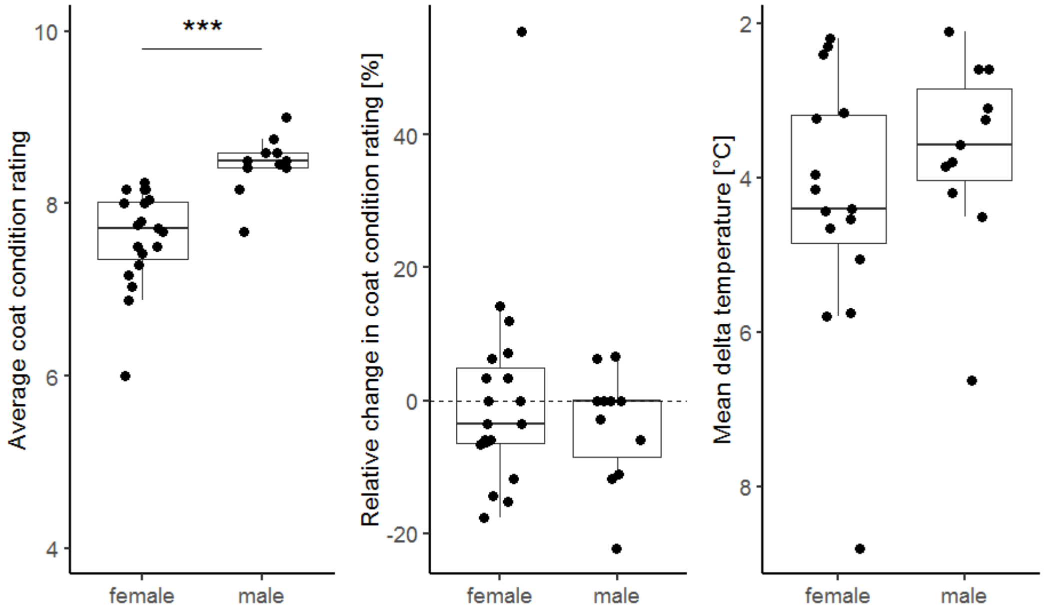


Figure 5.7 Coat condition measures by sex, with the average coat condition ratings of males and females in the left graph, the relative change in coat condition [%] in the middle (with the dashed line at zero indicating no change), and the mean delta coat temperature [°C] in the right graph (with the y-axis reversed, as smaller delta temperatures were assumed to reflect a more homogenous and thus better coat condition); asterisks indicate significance level: *** p < .0001 (average coat condition: t(27.93) = 5.20, p < .0001, CI = -1.19, -0.52).

Regarding effects of age, average coat condition did not differ between age classes for males (ANOVA, F(3,7) = 0.997, p = .448) or females (ANOVA, F(2,16) = 2.77, p = .093) when comparing means between age classes, but there was some evidence in the LMs used to investigate effects of rank and reproductive state that average coat condition might be worse in older compared to younger females (e.g. Table A V-I 3 in Appendix V-I, Figure 5.8). Mean changes in coat condition did not differ between age classes for males (ANOVA, F(3,7) = 0.48, p = .707) or for females (ANOVA, F(2,16) = 0.96, p = .405), and neither did mean delta coat temperature for males (ANOVA, F(3,7) = 0.24, p = .867) or females (ANOVA, F(2,12) = 0.24, p = .794).

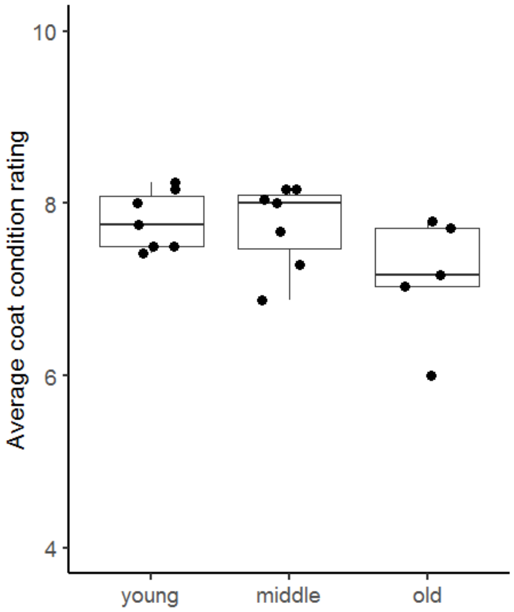


Figure 5.8 Females' average coat condition ratings in relation to their age class (ANOVA, F(2,16) = 2.77, p = .093, but age significant predictor of average coat condition in LM regarding the link between dominance rank and average coat condition rating: est. ± SE = -0.34 ± 0.15, p = .037, CI = -0.66, -0.02).

Finally, regarding the link between dominance rank position and coat condition measures, based on model comparisons there was some evidence that higher rank might be linked to better average coat condition in males and females (Figure 5.9), with Δ AIC_C < 2 of full models and full models explaining a larger part of variation in average coat condition than null models (Table 5.8, full details of models in Appendix V-I). While relative changes in coat condition did not differ with rank in males, model comparisons indicated that higher ranking females might have a worse development of coat condition over the dry season than lower ranking females (Figure 5.10). Delta coat temperatures, lastly, did not differ between dominance rank positions in either males or females.

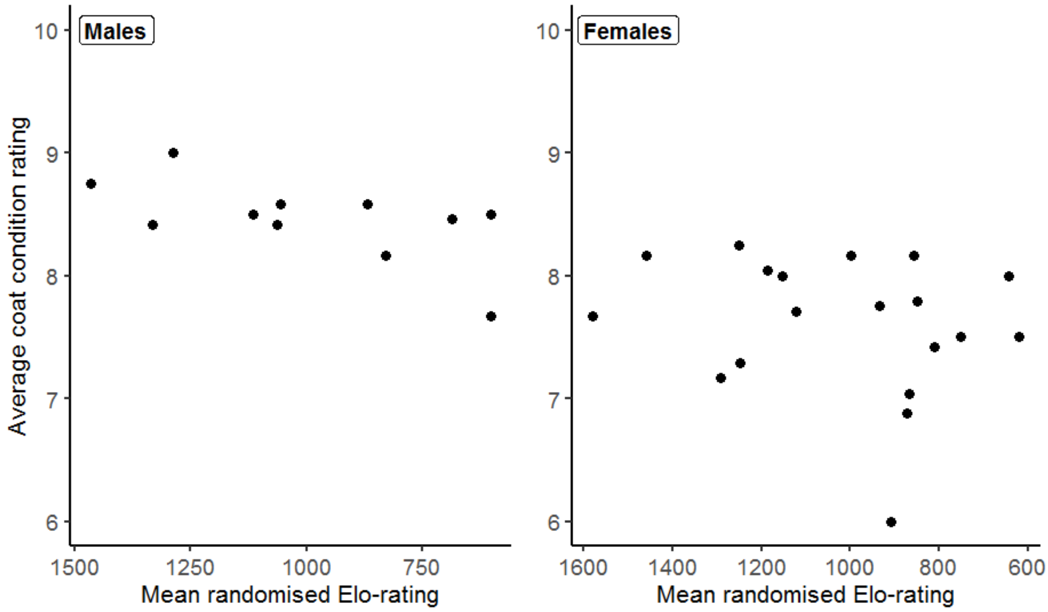


Figure 5.9 Males' average coat condition ratings on the left and females' average coat condition ratings on the right in relation to their dominance rank position, measured as mean randomised Elo-ratings. As high Elo-ratings reflect high dominance rank position, x-axes are reversed (males: Δ AIC_C = 1.57 and R^2 = 39.66%; females: Δ AIC_C = 1.2 and R^2 = 26.23%).

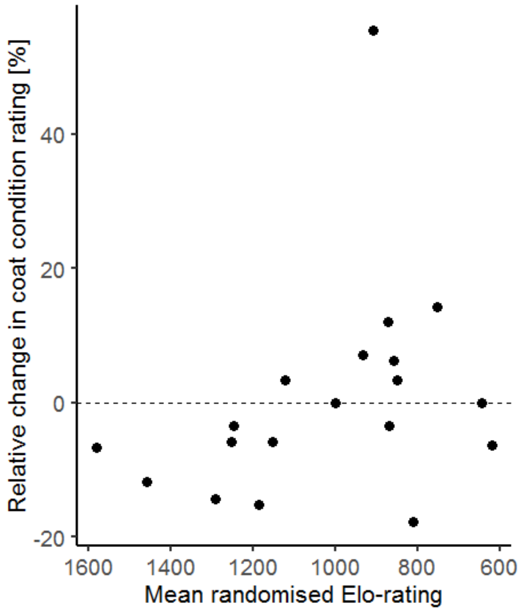


Figure 5.10 Females' relative change in coat condition ratings [%] over the dry season in relation to their dominance rank position, measured as mean randomised Elo-ratings (with the dashed line at zero indicating no change). As high Elo-ratings reflect high dominance rank position, the x-axis is reversed (Δ AIC_C = 0.17 and R^2 = 17.78%).

LM: *coat condition measure ~ rank measure + age*

Table 5.8 Results of LM comparisons regarding the link between males' and females' coat condition, measured as average coat condition, relative change in coat condition, and delta coat temperature, and their dominance rank position, measured as rank category and mean randomised Elo-ratings. Models included age class. Models with a Δ AIC$_C$ < 2 were considered to have received substantial support and are marked in bold and underlined.

	MALES						FEMALES					
	Response variable: (Δ AIC$_C$, marginal R^2 [%])											
	average coat cond.		**change in coat cond.**		**delta coat temp.**		**average coat cond.**		**change in coat cond.**		**delta coat temp.**	
Predictor:	**Δ AIC$_C$**	**R^2**	**Δ AIC$_C$**	**R^2**	**Δ AIC$_C$**	**R^2**	**Δ AIC$_C$**	**R^2**	**Δ AIC$_C$**	**R^2**	**Δ AIC$_C$**	**R^2**
rank category	2.6	34.51	4.43	13.5	4.46	5.54	**1.29**	**25.52**	**0.5**	**16.45**	3.54	2.49
rand. Elo-rating	**1.57**	**39.66**	4.07	15.83	4.76	3.46	**1.2**	**26.23**	**0.17**	**17.78**	3.79	1.09
null model	**0**	**21.52**	**0**	**9.04**	**0**	**0.02**	**0**	**19.05**	**0**	**5.08**	**0**	**1.01**

5.3.2 The calculation of resilience

As described above, resilience was defined as a 'relatively good outcome despite risk experiences' in the context of this study. Here, the 'good outcome' will be assessed based on the three measures of coat condition explained above (i.e. average coat condition, change in coat condition over the dry season, and delta coat temperature based on IRT measurements), while 'relative' will be understood both 'relative to other individuals' and 'relative to their demonstrated reactive scope'.

Demonstrated reactive scope describes the range of a mediator, here GC, the individual needs to utilise during a specific time period and as such reflects the energy demands an individual experiences based on their life-history stage and total volume of stressors they encounter. As such, low or high demonstrated reactive scope itself would neither be 'good' or 'bad' (even though, based on the allostasis model, a lower demonstrated reactive scope for the level of stressors an individual experiences is assumed to be beneficial due to the cost of 'wear and tear' connected to higher GC concentrations). The approach used here was therefore to assess whether individuals fared better or worse in their coat condition based on the expected coat condition for their demonstrated reactive scope.

For this purpose, LMs were constructed, containing one of the success measures as response variable and demonstrated reactive scope, measured as DRS or DRS_{CV}, as predictor. This way it was calculated for each individual whether their coat condition was above or below the predicted value for their demonstrated reactive scope. The residuals, i.e. the distance between observed and predicted values, were subsequently considered as the individuals' resilience (for a graphical depiction see for example Figure 5.11).

While the residuals could have also been calculated based on the reverse relationship, i.e. using demonstrated reactive scope as the response and the coat condition as the predictor variable, it seemed generally more likely that coat or body condition might be mediated by the GC system, than the reverse. However, a low coat quality might also lead to heightened energetic demands due to low insulation capacity and with it heightened GC responses to the cold, so using one as predictor and one as response variable does not imply a causal relationship here.

5.3.2.1 Calculating the resilience measures

As described above, resilience was calculated as the residuals, i.e. the difference between the observed and predicted values for individuals' coat condition based on their demonstrated reactive scope. In the following, the calculation of these residuals of all three success measures with each DRS and DRS_{CV} is depicted. As described above, average coat condition differed significantly between the sexes, so all resilience measures will be calculated separately for males and females.

Whether demonstrated reactive scope predicted coat condition was assessed using a model comparison approach, comparable to other analyses described in this thesis with the null model including age and dominance rank position as fixed effects and the full models additionally including either DRS or DRS_{CV}. For some coat condition measures (e.g. mean delta temperature), demonstrated reactive scope explained some of the variation in coat condition, while for others it did not (see Table 5.9, full model details in Appendix V-I). Nevertheless, all residuals were calculated based on simple linear models with the coat condition measure as the response variable and demonstrated reactive scope as predictor, as, even if the latter is not a statistically significant predictor, it might still explain a certain degree of variation in coat condition, and thus functions as a correction term for the variation in coat condition that might be explained by inter-individual differences in the physiological stress response system. Thus, while not all linear models were statistically significant, coat condition measures of individuals will be discussed as being ‘better’ or ‘worse’ than ‘predicted by demonstrated reactive scope’.

As residuals are potentially not easily interpretable depending on the coat condition measure, care was taken to construct linear models in a way that positive residuals always reflect high resilience: for average coat condition, this is straightforward, as higher coat condition is ‘better’ than lower coat condition; regarding relative change in coat condition, a large change is not necessarily bad, as some individuals increased in their ratings, while others decreased, thus it is the direction and magnitude of change that is reflected in the residuals; for delta coat temperatures, smaller delta values were assumed to be beneficial as they reflect a more homogenous coat cover, so here negative delta values were used in the linear model, as then positive residuals mean that the delta value is smaller than predicted – this way, positive residuals always reflect higher resilience.

LM: *coat condition measure ~ DRS or DRS$_{CV}$ + mean rand. Elo-rating + age*

Table 5.9 Results of LM comparisons regarding the link between coat condition measures (average coat condition, relative change in coat condition, and mean delta coat temperature) and demonstrated reactive scope (measured as DRS and DRS$_{CV}$) of males and females. Models included age and mean randomised Elo-ratings as a measure of dominance rank position. Models with a Δ AIC$_C$ < 2 or strikingly large effect sizes were considered to have received substantial support and are marked in bold and underlined.

	MALES						FEMALES					
	Response variable: (Δ AIC$_C$, marginal R^2 [%])											
	aver. coat cond.		**change in coat cond.**		**delta coat temp.**		**aver. coat cond.**		**change in coat cond.**		**delta coat temp.**	
Predictor:	**Δ AIC$_C$**	**R^2**	**Δ AIC$_C$**	**R^2**	**Δ AIC$_C$**	**R^2**	**Δ AIC$_C$**	**R^2**	**Δ AIC$_C$**	**R^2**	**Δ AIC$_C$**	**R^2**
DRS$_{CV}$	7.27	36.77	7.33	14.17	**5.01**	**16.87**	2.39	29.6	**0**	**30.71**	**0.58**	**20.58**
DRS	7.31	36.59	7.32	14.19	6.34	9.11	3.72	25.12	2.18	23.35	3.59	6.46
null model	**0**	**39.66**	**0**	**15.83**	**0**	**3.46**	**0**	**26.23**	**0.21**	**17.78**	**0**	**1.09**

Regarding average coat condition, full models including DRS$_{CV}$ or DRS did not receive substantial support in the model comparison, potentially due to a large percentage of variation in this measure, i.e. nearly 40% for males and 26% for females, already being explained by age and dominance rank position. Residuals of all four models (i.e. average coat condition ~ DRS or DRS$_{CV}$) are shown in Figure 5.11. Here, a positive residual indicates a better ‘than predicted’ overall coat condition, while a negative residual reflects worse coat condition than predicted by their demonstrated reactive scope.

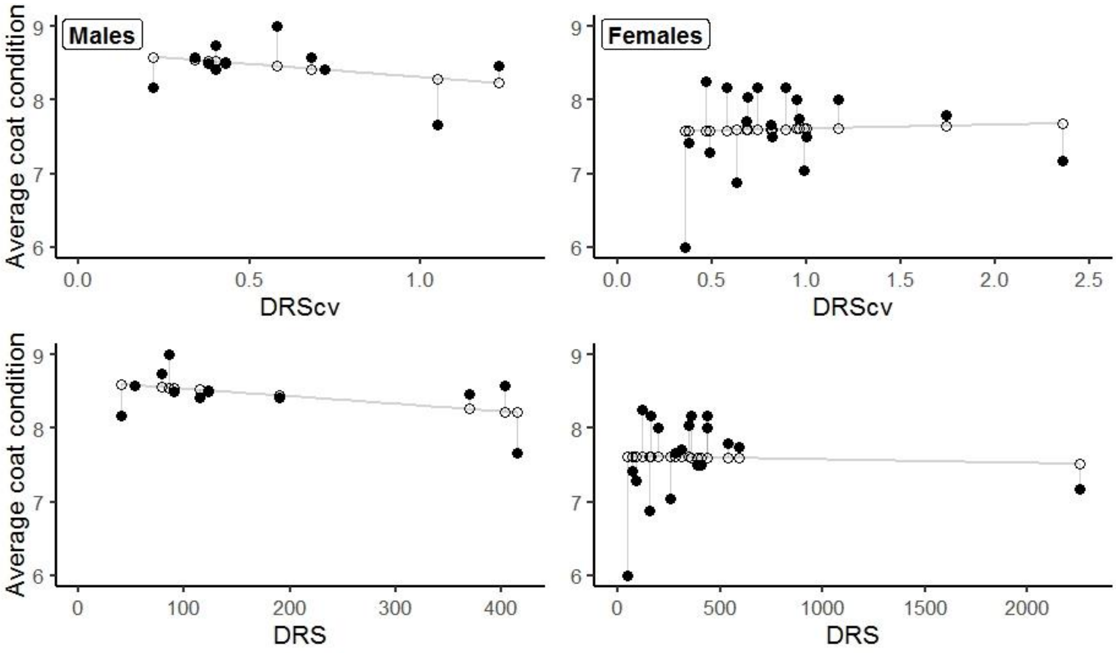


Figure 5.11 Males' (left) and females' (right) average coat condition in relation to their demonstrated reactive scope, measured as DRS_{CV} (top graphs) and DRS (bottom graphs). White circles represent the predicted average coat condition (based on simple LMs with average coat condition as response variable and DRS or DRS_{CV} as predictor), while black circles show the observed average coat condition, with vertical lines in between representing the residuals. Predicted values are linked by a regression line based on the linear model.

Concerning the relative change in coat condition, full models did also not receive any substantial support in the model comparison for males, but for females the full model including DRS_{CV} was the best model of the set, with the null model also receiving substantial support. Here, the full model explained about 30% of variation in the relative change in coat condition, compared to the 17% of the null model. Residuals based on the simple linear models are shown in Figure 5.12. For females, some linear model assumptions were not fulfilled, suggesting a potential non-linear relationship between the variables and a skew in the response variable.

Generally, negative values of relative change indicate a worsening of coat condition over the rating period, while positive values indicate an improvement, with zero indicating no change from first to last rating. As Figure 5.12 shows, for the most part individuals with unchanged or improved coat condition also had better development in coat condition than predicted based on their DRS or DRS_{CV}, leading to positive residuals and thus positive resilience scores; individuals with worsening coat condition from the first to the last rating mostly had worse than predicted changes and thus negative resilience values.

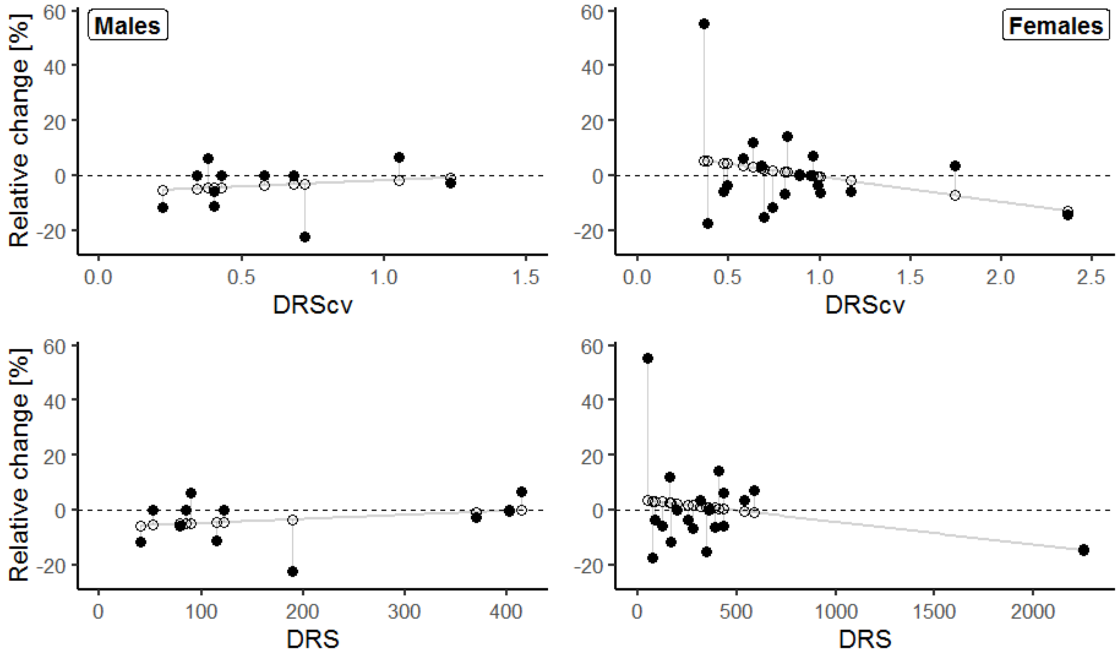


Figure 5.12 Males' (left) and females' (right) relative change in coat condition [%] in relation to their demonstrated reactive scope, measured as DRS_{CV} (top graphs) and DRS (bottom graphs). White circles represent the predicted relative change in coat condition (based on simple LMs with relative change in coat condition as response variable and DRS or DRS_{CV} as predictor), while black circles show the observed change in coat condition over the dry season, with vertical lines in between representing the residuals. Predicted values are linked by a regression line based on the linear model. The dashed line at y = 0 indicates measures of unchanged coat condition, while positive values indicate that an individual's coat condition increased over the dry season, and negative values indicate that the coat condition decreased.

Regarding delta coat temperatures, smaller delta values were considered to be 'beneficial' compared to larger delta values as they represent a more homogeneous coat cover. Therefore, as described above, negative delta values were used for the calculation of residuals, so that small delta values are more positive than predicted, while larger delta values are worse or 'more negative' than predicted based on DRS or DRS_{CV}, as is shown in Figure 5.13.

For both males and females, full models including DRS_{CV} received substantial support in the model comparison: for males, while the Δ AICC > 2, the full model explained 13% more of the variation in this coat condition measure than the null model did (i.e. nearly 17% compared to the 3.5% of the null model); for females, the full model had a Δ AICC < 2, with the null model having the lowest AIC_C, but here the full model explained over 20% of variation compared to the 1% of the null model. Residuals calculated based on the simple LM of mean delta coat temperature by demonstrated reactive scope are shown in Figure 5.13.

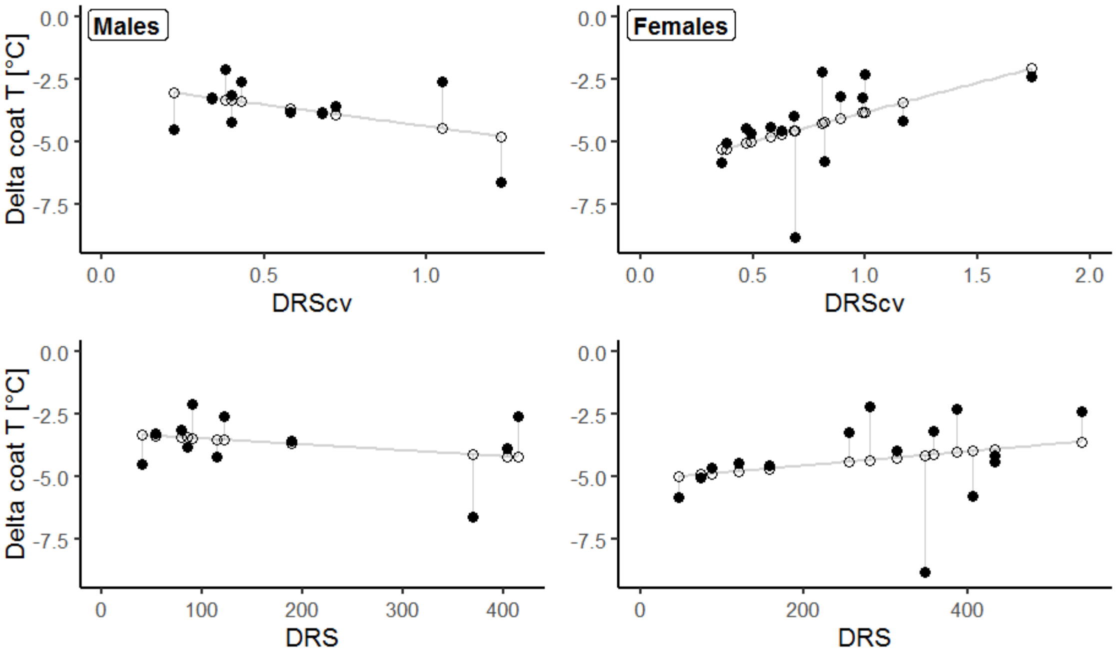


Figure 5.13 Males' (left) and females' (right) mean delta coat temperature [°C] in relation to their demonstrated reactive scope, measured as DRS_{CV} (top graphs) and DRS (bottom graphs). White circles represent the predicted mean delta coat temperature (based on simple LMs with mean delta coat temperature as response variable and DRS or DRS_{CV} as predictor), while black circles show the observed mean delta coat temperatures, with vertical lines in between representing the residuals. Predicted values are linked by a regression line based on the linear model. Delta coat temperatures are depicted as negative values, as small delta values are assumed to be beneficial as they reflect a more homogenous coat cover and thus a better insulating coat, thus aiding in the easier interpretation of residuals where positive residuals (i.e. observed values lie above the regression line) reflect higher resilience than 'worse than predicted' delta coat temperatures, where the observed value lies below the regression line.

5.3.2.2 Relation between resilience measures and their terminology

To explore whether these different measures of resilience are linked to each other, pair-wise correlation tests were conducted. Here, only resilience measures based on the same measure of coat condition (e.g. average coat condition by DRS and average coat condition by DRS_{CV}) were highly and significantly correlated, while residuals based on different success measures were not (Table 5.10). Therefore, three measures of resilience based on the three success measures in relation to DRS_{CV} will be used for the following analyses, as in all cases DRS_{CV} was found to be a better predictor of coat condition in the model comparison above, and based on the assumption that results would be highly similar if DRS were used instead. The three measures will be termed as follows:

R_{coat}: Residuals calculated as the difference between observed and predicted values of average coat condition based on the individuals' DRS_{CV}. A positive R_{coat} thus represents a better than predicted average coat condition for the respective DRS_{CV}, while a negative R_{coat} reflects a worse than predicted average coat condition.

R_{change}: Residuals calculated as the difference between observed and predicted relative changes in coat condition based on the individuals' DRS_{CV}. As some individuals improved in their coat condition ratings over the months while others decreased, a positive R_{change} indicates a more positive than expected development in coat condition ratings based on their DRS_{CV}, i.e. in most cases either increased or unchanged ratings, while negative R_{change} values reflect a worse than predicted change in coat condition based on their DRS_{CV} values, i.e. in most cases a decrease in coat condition.

R_{temp}: Residuals calculated as the difference between observed and predicted delta coat temperatures based on the individuals' DRS_{CV}. As small delta coat temperature values were thought to reflect a more homogenous coat (as the difference between maximum and minimum measured temperatures was smaller), all delta coat temperatures were used as negative values, so that 'smaller' (or less negative) than based on the DRS_{CV} predicted delta values led to positive residuals.

Overall, positive R_{coat}, R_{change}, and R_{temp} reflect better than predicted coat condition measures (and thus positive resilience), either reflecting a better than predicted average rating, a more positive development of coat condition, or a smaller delta coat temperature and thus a more homogeneous coat, than predicted based on the individuals' DRS_{CV}. Generally, R_{coat} will be assumed to represent the individuals' long-term resilience as coat condition develops over long time periods; R_{change} is thought to reflect resilience on a shorter timescale and, more specifically, the ability to cope with the challenges during the dry season; while R_{temp} represents an objective, quantitative assessment of individuals' resilience at the end of the study period and end of dry season. Whether these measures of resilience are linked to different aspects of individuals' life-history stage, behaviour, or sociability will be investigated below.

Table 5.10 Correlation coefficients between residuals calculated as measures of resilience, analysed separately for males (M) and females (F). For females, Spearman's rank correlations were used as residuals were not normally distributed, while for males Pearson's product-moment correlations were used. Highly correlated residuals (r > 0.6) are marked in bold and underlined.

	Average coat cond. x DRS_{CV}	Rel. change in coat cond. x DRS	Rel. change in coat cond. x DRS_{CV}	Delta coat temp. x DRS	Delta coat temp. x DRS_{CV}
Average coat cond. x DRS	**F: r = 0.996** **M: r = 0.97**	F: r = -0.30 M: r = 0.05	F: r = -0.26 M: r = 0.04	F: r = 0 M: r = -0.24	F: r = 0.14 M: r = -0.23
Average coat cond. x DRS_{CV}		F: r = -0.31 M: r = 0.03	F: r = -0.27 M: r = -0.01	F: r = 0 M: r = -0.31	F: r = 0.14 M: r = -0.27
Rel. change in coat cond. x DRS			**F: r = 0.99** **M: r = 0.99**	F: r = -0.25 M: r = 0.45	F: r = -0.29 M: r = 0.45
Rel. change in coat cond. x DRS_{CV}				F: r = -0.17 M: r = 0.47	F: r = -0.28 M: r = 0.47
Delta coat temp. x DRS					**F: r = 0.8** **M: r = 0.97**

5.3.2.3 Inter-individual variation and sex differences in resilience measures

Variation in resilience measures between individuals are depicted for males in Figure 5.14 and for females in Figure 5.15. As described above, resilience measures were not correlated with each other, as can also be seen in these figures, and thus potentially reflect different aspects of resilience. To investigate whether males and females differed in their resilience, the three measures of resilience based on DRS_{CV} values were compared. Males and females did not differ in their R_{coat} (Mann-Whitney U test, W = 96, p = .731, CI = -0.41, 0.3), their R_{change} (Mann-Whitney U test, W = 119, p = .553, CI = -5.79, 9.60), or their R_{temp} (Mann-Whitney U test, W = 73, p = .646, CI = -1.06, 0.73). Nevertheless, to keep comparability with other analyses, all analyses conducted in this chapter were conducted separately for males and females.

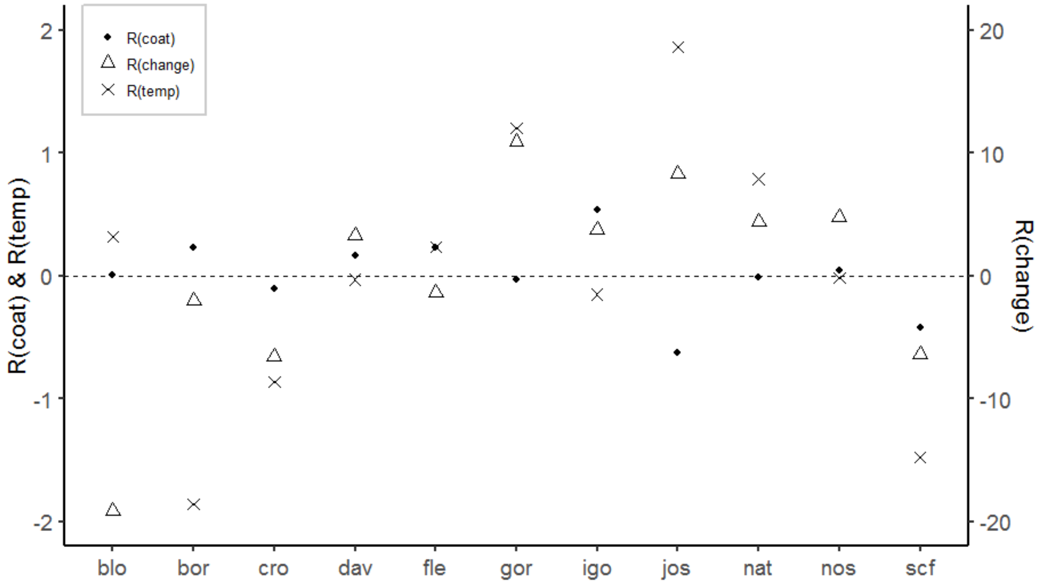


Figure 5.14 Individual measures of resilience of all males in alphabetical order, with R_{coat} and R_{temp} indicated on the primary y-axis, and R_{change} indicated on the secondary y-axis. Shape shows resilience measure, as indicated by the legend.

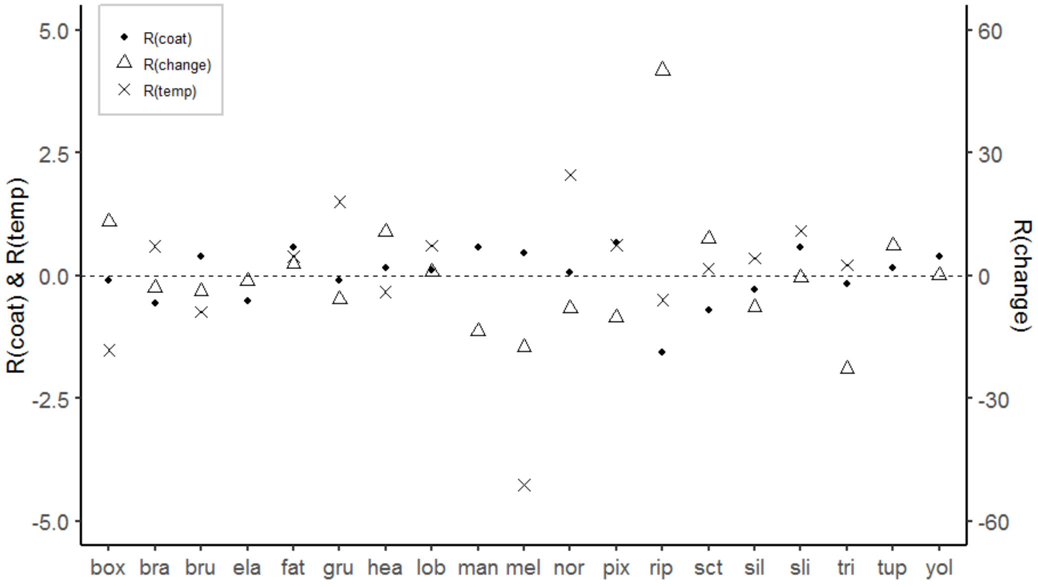


Figure 5.15 Individual measures of resilience of all females in alphabetical order, with R_{coat} and R_{temp} indicated on the primary y-axis, and R_{change} indicated on the secondary y-axis. Shape shows resilience measure, as indicated by the legend.

5.4 Results Part II: Investigating resilience

5.4.1 Demographic factors

Hypothesis 1: Measures of resilience are linked to demographic factors.

Prediction 1i: Resilience decreases with age.

For males, there was no significant difference between age classes in their R_{coat} (ANOVA, F(3,7) = 1.12, p = .405), their R_{change} (ANOVA, F(3,7) = 0.31, p = .818), or their R_{temp} (ANOVA, F(3,7) = 0.725, p = .569). Similarly, for females, there was no significant difference in means between age classes in R_{coat} (ANOVA, F(2,16) = 3.08, p = .074), in R_{change} (ANOVA, F(2,16) = 2.23, p = .140), or in R_{temp} (ANOVA, F(2,12) = 0.04, p = .961). However, in all subsequent models of females' R_{coat}, age was a significant negative predictor of this resilience measure, indicating that while means might not significantly differ between age classes, R_{coat} seems to decrease with increasing age. In the null model of the following analysis regarding the link between dominance rank position and R_{coat}, age explained about 20% of variation in this resilience measure (Table A V-II 4 in Appendix V-II; Figure 5.16).

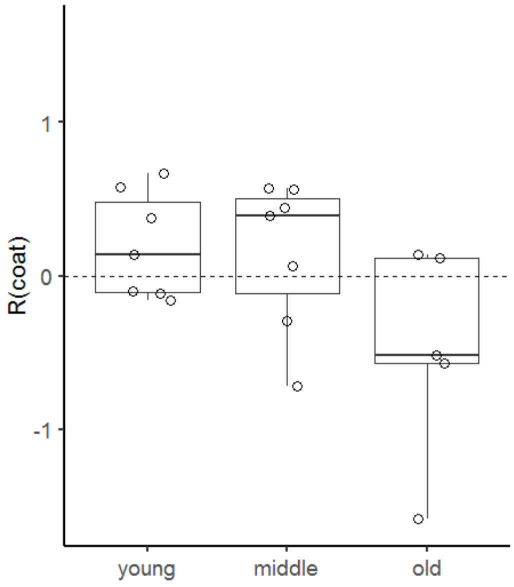


Figure 5.16 Females' resilience measured as R_{coat} in relation to their age class (ANOVA, F(2,16) = 3.08, p = .074, but significant predictor of R_{coat} in LM regarding the link between dominance rank and R_{coat}: est. ± SE = -0.32 ± 0.15, p = .046, CI = -0.64, -0.01).

Prediction 1ii: High-ranking individuals are more resilient than low-ranking individuals.

To investigate if dominance rank position was linked to resilience, LMs were constructed using either rank category or mean randomised Elo-ratings as predictor variable and compared to null models, in a comparable manner to analyses in chapter 3. All models included age. Results of model comparisons are compiled in Table 5.11, while model details can be found in Appendix V-II.

Males' resilience measures were not linked to their dominance rank position, measured either as mean randomised Elo-rating or rank category: there was no link between either rank measure and R_{coat}, or R_{change}, or R_{temp} as in all cases the null models were the best models, with all full models having a Δ $AIC_C > 2$. In the case of R_{coat}, though, the full models did explain an additional 10% of variation in resilience.

For females' R_{coat}, the null model was the best model of the set and 1.7 times as likely to be the best model compared to the best full model, but all Δ AIC_C were below 2. Here, full models indicate that higher rank was linked to higher R_{coat} (Figure 5.17). Regarding R_{change} and R_{temp}, some model assumptions were violated, hinting at non-normal distributions and possible non-linear relationships between predictors and response variable. For R_{change}, all full models were as good as the null model in explaining variation in resilience, i.e. all Δ $AIC_C < 2$. While the null model did have the lowest AIC_C, full models explained an additional 13% of variation compared to the null model. These results indicate that lower ranking females had higher R_{change} than higher-ranking females (Figure 5.18). For R_{temp}, the null model was the best model with all Δ $AIC_C > 2$, and neither age nor dominance rank position explained any variation.

LM: *resilience measure ~ rank measure + age class*

Table 5.11 Results of LM comparisons regarding the link between males' and females' resilience, measured as R_{coat}, R_{change}, and R_{temp}, and their dominance rank position, measured as rank category and mean randomised Elo-ratings. Models included age class. Models with a Δ $AIC_C < 2$ were considered to have received substantial support and are marked in bold and underlined.

	MALES						FEMALES					
	Response variable: (Δ AIC_C, marginal R^2 [%])											
	R_{coat}		**R_{change}**		**R_{temp}**		**R_{coat}**		**R_{change}**		**R_{temp}**	
Predictor:	**Δ AIC_C**	**R^2**	**Δ AIC_C**	**R^2**	**Δ AIC_C**	**R^2**	**Δ AIC_C**	**R^2**	**Δ AIC_C**	**R^2**	**Δ AIC_C**	**R^2**
rank category	3.19	25.19	4.59	10.38	4.69	6.07	**1.21**	**27.11**	**0.14**	**24.69**	3.77	0.27
rand. Elo-rating	3.04	27.05	4.44	11.38	5.16	2.75	**1.04**	**27.72**	**0**	**25.18**	3.76	0.32
null model	**0**	**15.18**	**0**	**6.61**	**0**	**2.47**	**0**	**20.52**	**0.45**	**11.25**	**0**	**0.002**

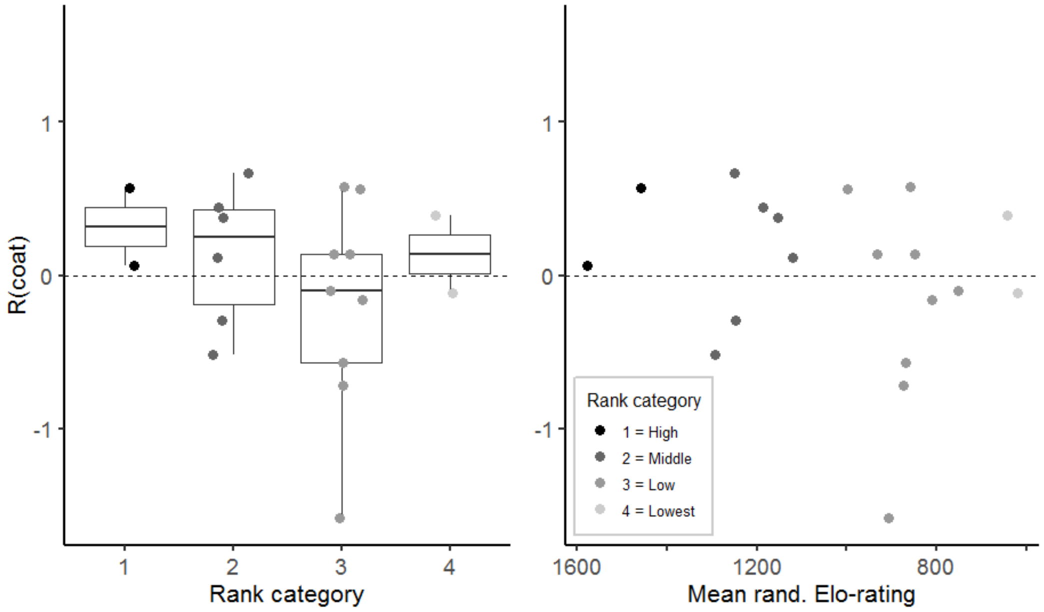


Figure 5.17 Females' resilience measured as R_{coat} in relation to rank category on the left, and mean randomised Elo-rating on the right (rank category: Δ AIC_C = 1.21 and R^2 = 27.11%; mean randomised Elo-rating: Δ AIC_C = 1.04 and R^2 = 27.72%).

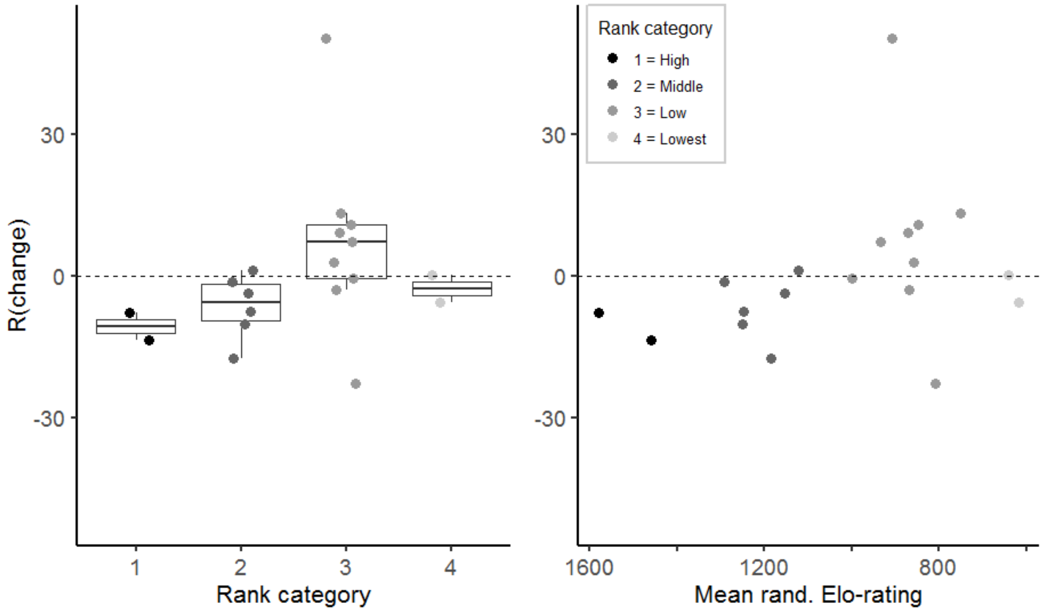


Figure 5.18 Females' resilience measured as R_{change} in relation to their rank category on the left, and mean randomised Elo-rating on the right (rank category: Δ AIC_C = 0.14 and R^2 = 24.69%; mean randomised Elo-rating: Δ AIC_C = 0 and R^2 = 25.18%).

5.4.2 Reproduction and mean physiological stress response levels

Hypothesis 2: Resilience is linked to reproduction and mean physiological stress response levels.

Prediction 2i: Individuals with lower resilience have higher mean fGCM concentrations.

To investigate if high mean physiological stress response levels were linked to lower resilience, full models including mean fGCM concentrations were compared to null models, which only included age and rank category. Results of model comparisons are presented in Table 5.12, while model details are shown in Appendix V-III.

For males, none of the full models investigating R_{coat}, R_{change} or R_{temp} received any support, as all Δ $AIC_C > 2$.

For females, some linear model assumptions were violated, indicating that R_{change} might not be normally distributed, and that there might be a non-linear relationship between predictor and response variable. Only the full model regarding R_{temp} received some support, with a Δ AIC_C of 1.75 and an effect size of nearly 15% compared to < 1% of the null model, indicating that females with higher mean fGCM concentrations had lower resilience (Figure 5.19). None of the full models regarding R_{coat} or R_{change} received support in the model comparisons.

LM: *resilience measure ~ mean fGCM concentration + age class + rank category*

Table 5.12 Results of LM comparisons regarding the link between males' and females' resilience, measured as R_{coat}, R_{change}, and R_{temp}, and their mean fGCM concentrations. Models included age and rank categories. Models with a Δ AIC_C < 2 were considered to have received substantial support and are marked in bold and underlined.

	MALES						FEMALES					
	Response variable: (Δ AIC_C, marginal R^2 [%])											
	R_{coat}		**R_{change}**		**R_{temp}**		**R_{coat}**		**R_{change}**		**R_{temp}**	
Predictor:	**Δ AIC_C**	**R^2**	**Δ AIC_C**	**R^2**	**Δ AIC_C**	**R^2**	**Δ AIC_C**	**R^2**	**Δ AIC_C**	**R^2**	**Δ AIC_C**	**R^2**
mean fGCM conc.	7.07	25.10	7.33	9.22	7.19	6.17	3.38	27.12	3.75	23.54	**<u>1.75</u>**	**<u>14.68</u>**
null model	**<u>0</u>**	**<u>26.19</u>**	**<u>0</u>**	**<u>10.38</u>**	**<u>0</u>**	**<u>6.07</u>**	**<u>0</u>**	**<u>27.11</u>**	**<u>0</u>**	**<u>24.69</u>**	**<u>0</u>**	**<u>0.27</u>**

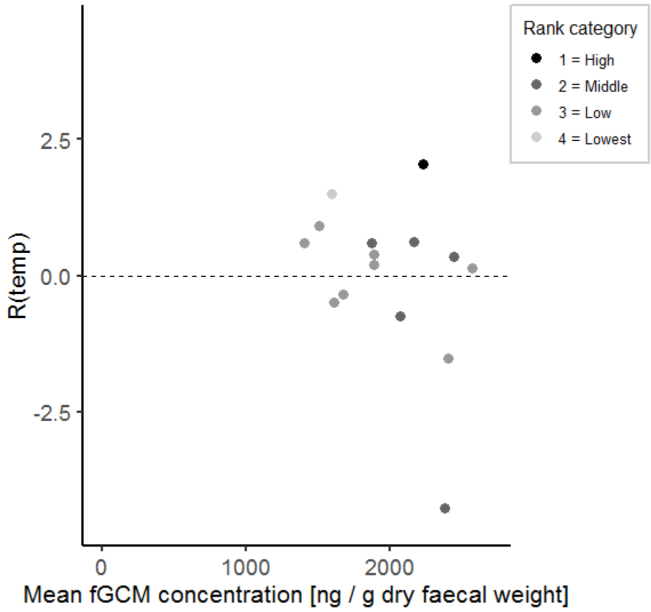


Figure 5.19 Females' resilience measured as R_{temp} in relation to their mean fGCM concentration [ng/g dry faecal weight] (Δ AIC_C = 1.75 and R^2 = 14.68%).

Prediction 2ii: Females that were lactating during the study period have lower resilience, linked to energetic trade-offs.

When investigating the link between reproductive factors and resilience in females in an energetic trade-off context, full models were compared that included either the number of infants that survived at least until one year of age (between 0 and 2 infants) or whether the females were lactating at some point during the study period (factor yes/no). Full models were compared to null models only including age and rank. Results of model comparisons are collated in Table 5.13, while full model details can be found in Appendix V-III.

For all three measures of resilience, the full models including the number of surviving infants received substantial support, with all Δ $AIC_C < 2$. As Figure 5.20 shows, the direction of the associations went into different directions though: females with more surviving infants had higher R_{coat}, but lower R_{change} and R_{temp}. In the latter case, though, infrared pictures were only available for one female that had two surviving infants, so the result is not reliable. Additionally, the full models including the factor of whether females were lactating received support for R_{change} and R_{temp}. For R_{change}, though, the Δ AIC_C was only below 2 after an influential data point was removed, and Figure 5.21 shows no clear differences depending on whether they were lactating. Figure 5.21 and Table 5.13 also suggest that single data points might explain the link found between lactation and R_{temp} as well, potentially linked to small sample sizes.

LM: *resilience measure ~ reproductive factor + age class + rank category*

Table 5.13 Results of LM comparisons regarding females' resilience, measured as R_{coat}, R_{change}, and R_{temp}, using the number of surviving infants and whether they were lactating (yes/no) as predictors. Models included age and rank categories. Models with a Δ $AIC_C < 2$ were considered to have received substantial support and are marked in bold and underlined. When influential data points were detected, models were run again without these data points and compared to the respective null model, the results are shown in brackets; if full models had different individuals as influential data points, a new null model was calculated for each case and comparisons are marked by superscript numbers.

	FEMALES					
	Response variable: (Δ AIC_C, marginal R^2 [%])					
	R_{coat}		**R_{change}**		**R_{temp}**	
Predictor:	**Δ AIC_C**	**R^2**	**Δ AIC_C**	**R^2**	**Δ AIC_C**	**R^2**
no. of surviving infants	**0**	**47.34**	**1.51**	**31.07**	**0.72** (4.83	**19.34** 4.92)^1
lactating	6.73	27.65	3.46 **(0.25**	24.54 **30.66)**	**1.77** (4.46	**14.55** 31.87)^2
null model	3.5	27.11	**0** **(0**	**24.69** **18.28)**	**0** **(0** **(0**	**0.27** **4.08)^1** **29.01)^2**

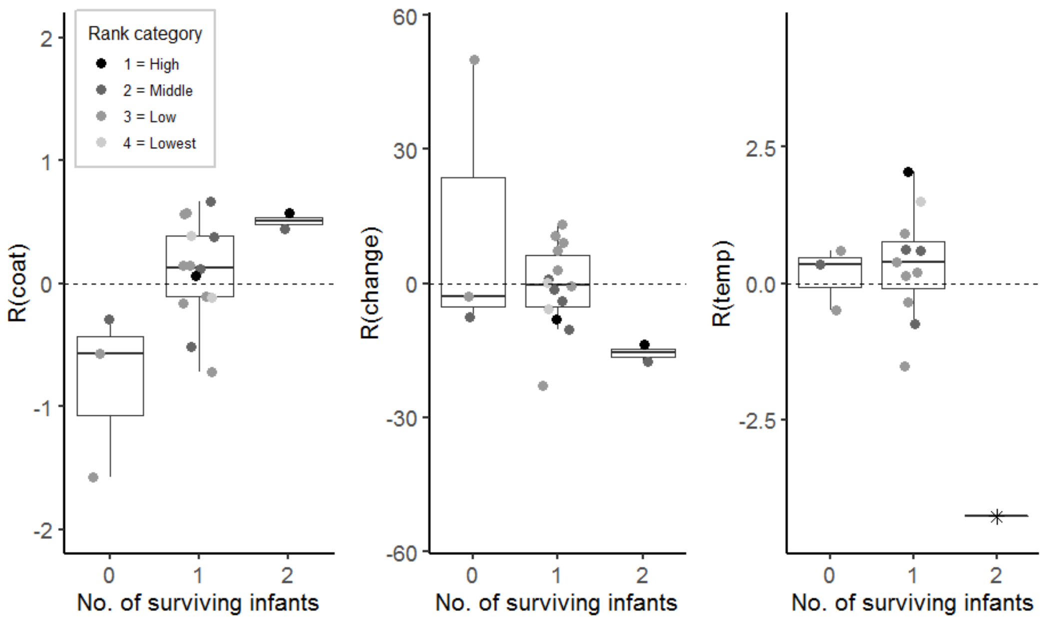


Figure 5.20 Females' resilience measured as R_{coat} on the left, R_{change} in the middle, and R_{temp} on the right in relation to the number of surviving infants they had in the last three years (R_{coat}: $\Delta AIC_C = 0$ and $R^2 = 47.34\%$; R_{change}: $\Delta AIC_C = 1.51$ and $R^2 = 31.07\%$; R_{temp}, with the influential data point (marked *): $\Delta AIC_C = 0.72$ and $R^2 = 19.34\%$; without the influential data point: $\Delta AIC_C = 4.83$ and $R^2 = 4.92\%$).

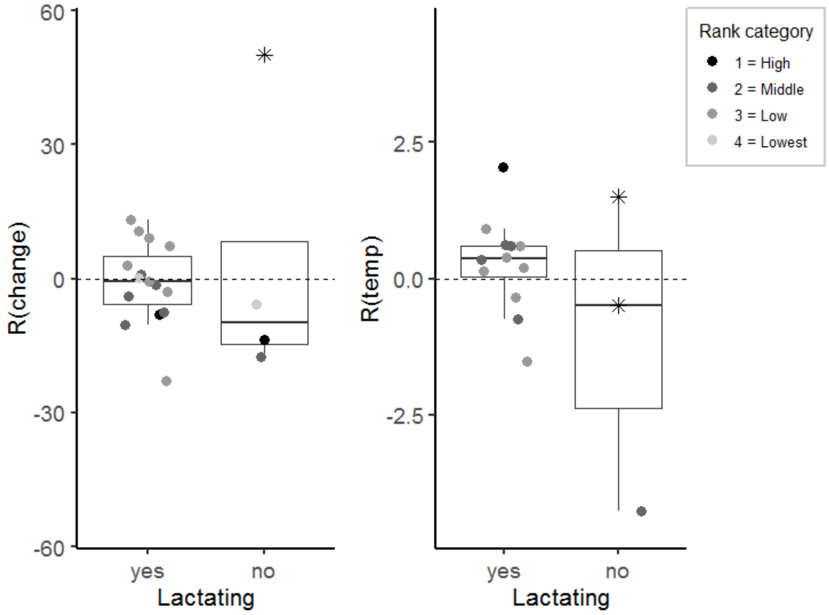


Figure 5.21 Females' resilience measured as R_{change} on the left and R_{temp} on the right in relation to whether they were lactating during the study period (R_{change}, with the influential data point (marked *): $\Delta AIC_C = 3.46$ and $R^2 = 24.54\%$, without the influential data point: $\Delta AIC_C = 0.25$ and $R^2 = 30.66\%$; R_{temp}, with the influential data points (marked *): $\Delta AIC_C = 1.77$ and $R^2 = 14.55\%$, without the influential data points: $\Delta AIC_C = 4.46$ and $R^2 = 31.87\%$).

Prediction 2iii: Females that lost an infant in the last three years have lower resilience.

In addition to the energetic demands posed by caring for an infant, the loss of an infant might also be a major stressor for a female. Thus, losing an infant might be connected to subsequently lower resilience, or females with lower resilience might be less able to care for their infant and thus have a higher probability of losing it in the first year. For this investigation, a full model was constructed including the factor of whether the females had lost at least one infant in the last three years (factor yes/no). Some model assumptions were violated regarding the models of R_{change} and R_{temp}, suggesting a non-normal distribution of response variables and a non-linear relationship between predictor and response variable. Full models were compared to null models only including age and rank. Results of model comparisons are collated in Table 5.14, while full model details can be found in Appendix V-III.

The only full model to receive substantial support was the model for R_{coat}. Here, both the full and the null model had $\Delta\,\mathrm{AIC_C} < 2$, but the full model explained an additional 9% of variation in R_{coat} compared to the null model. Based on this model, females who had lost at least one infant had lower R_{coat} than females who did not lose any infants in the last three years (Figure 5.22).

LM: *resilience measure ~ lost an infant (yes/no) + age class + rank category*

Table 5.14 Results of LM comparisons regarding females' resilience, measured as R_{coat}, R_{change}, and R_{temp}, using the factor of whether they lost an infant in the last three years (yes/no) as predictor. Models included age and rank categories. Models with a $\Delta\,\mathrm{AIC_C} < 2$ were considered to have received substantial support and are marked in bold and underlined.

	FEMALES					
	Response variable: ($\Delta\,\mathrm{AIC_C}$, marginal R^2 [%])					
	R_{coat}		**R_{change}**		**R_{temp}**	
Predictor:	**$\Delta\,\mathrm{AIC_C}$**	**R^2**	**$\Delta\,\mathrm{AIC_C}$**	**R^2**	**$\Delta\,\mathrm{AIC_C}$**	**R^2**
lost an infant	**0.55**	**36.15**	3.4	24.76	4.61	0.48
null model	**0**	**27.11**	**0**	**24.69**	**0**	**0.27**

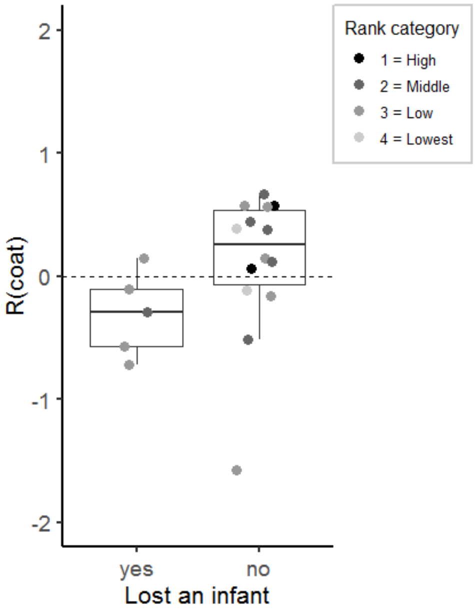


Figure 5.22 Females' resilience measured as R_{coat} in relation to whether they lost at least one infant in the last three years (Δ AIC_C = 0.55 and R^2 = 36.15%).

5.4.3 Social and behavioural mediation of resilience

Hypothesis 3: Resilience is behaviourally or socially mediated.

Prediction 3i: High resilience is linked to high rates of self-directed/affiliative/ agonistic behaviour, reflecting behavioural resilience.

To investigate if potential coping behaviours are linked to measures of resilience, the same behavioural rates used in chapter 4 were included as predictor variables in full models and compared to null models, which only included age and rank category. Results of the model comparisons are compiled in Table 5.15, while full model details can be found in Appendix V-IV.

For males, there was high multicollinearity between rates of giving grooming and rank, so rank was excluded from the respective models. None of the full models received any substantial support in explaining variation in R_{coat}. However, the full model including rates of giving grooming and the null model received substantial support regarding R_{change}, in that males that groomed more had higher resilience (Figure 5.23). Regarding

R_{temp}, the full models including rates of scratching and total self-directed behaviour were the best models and explained more than 50% of variation in resilience. Males that performed more scratching or other self-directed behaviours had a higher resilience than males who showed these behaviours at lower rates (Figure 5.24). In all other full models of R_{temp}, one adolescent male was an influential data point. For comparability reasons, all models of R_{temp} were calculated again without this data point; subsequently, there was high multicollinearity between behavioural rates and age or rank in several models (details in Appendix V-IV), so either age or rank as indicated in the respective tables in the Appendix were excluded. Nevertheless, the full model containing rates of scratching was the best models of the set in explaining variation in R_{temp}.

Regarding females, there were some problems with the linear model assumptions, suggesting that R_{change} and R_{temp} might not be normally distributed, and that there might be non-linear relationships between these response variables and fixed effects. Additionally, there was high multicollinearity between rates of aggression as well as general rates of agonism, and rank, so rank was excluded from the respective models. For the models on R_{coat}, both the full models including rates of scratching and total self-directed behaviour, as well as the full model including rates of receiving grooming received substantial support, as all Δ $AIC_C < 2$, and these models explained more than 40% of variation in this resilience measure. For both scratching and self-directed behaviour, though, in contrast to prediction, the association was negative, so females that scratched more or showed higher rates of all self-directed behaviour had lower resilience (Figure 5.25), while the association of R_{coat} to rates of receiving grooming was positive and thus in line with the prediction, indicating that females who received grooming at higher rates had a higher R_{coat} (Figure 5.26). Regarding R_{change}, the full models including aggression and agonism rates received substantial support in relation to the null model but did not explain more variation in resilience than the null model already did. As high-ranking females tended to have lower R_{change} than lower ranking females as well as showing higher rates of aggression, it is not possible to differentiate between the effects of rank and aggression rates. Either way, though, high rates of aggression were linked to lower R_{change}, which is in contrast to the prediction (Figure 5.26). Concerning R_{temp}, as for males, the full models containing scratching and all self-directed behaviours received substantial support and explained over 30% of variation in resilience. Additionally, the agonism model received some support but only explained about 5% of variation. There was one influential data point in the model for rates of giving grooming, so to be able to compare models, the full models containing giving grooming, scratching, self-directed behaviour, as well as the null model were recalculated without this female. Only the scratching and self-directed behaviour models retained substantial support in relation to the null model. Here, the associations were positive, in that females who scratched more or showed higher rates of all self-directed behaviour had higher R_{temp}, consistent with the findings in males and predictions (Figure 5.27), but contrary to the finding of a negative link between rates of self-directed behaviour and R_{coat} in females described above.

LM: *resilience measure ~ behavioural rate + age class + rank category*

Table 5.15 Results of LM comparisons regarding the link between long-term rates of behaviour and resilience measures (R_{coat}, R_{change}, and R_{temp}) of males and females. Models included age and rank category. Models with a Δ AIC_C < 2 were considered to have received substantial support and are marked in bold and underlined. Numbers in brackets represent model comparison results once influential data points (Cook's distance > 1) were removed.

	MALES						FEMALES					
	Response variable: (Δ AIC_C, marginal R^2 [%])											
	R_{coat}		**R_{change}**		**R_{temp}**		**R_{coat}**		**R_{change}**		**R_{temp}**	
Predictor behaviour:	**Δ AIC_C**	**R^2**	**Δ AIC_C**	**R^2**	**Δ AIC_C**	**R^2**	**Δ AIC_C**	**R^2**	**Δ AIC_C**	**R^2**	**Δ AIC_C**	**R^2**
scratching	6.13	29.95	8.04	9.21	**0.95** **(0**	**52.59** **45.22)**	**0**	**43.81**	3.7	25.76	**0.65** **(1.42**	**31.68** **28.95)**
self-directed behaviour	4.72	36.79	8.02	9.33	**0** (6.45	**55.99** 52.53)	**0.66**	**42.02**	3.67	25.85	**0** **(0.83**	**34.17** **31.43)**
giving grooming	2.02	13.9	**0**	**15.03**	3.74 (2.09	2.33 34.33)	4.76	29.69	4.34	23.55	7.56 (3.55	0.25 19.42)
receiving grooming	7.01	25.43	8.01	9.41	9.49 (6.32	11.66 6.90)	**0.26**	**43.11**	4.33	23.56	6.56	5.35
aggression	7.04	25.28	7.61	11.76	10.25 (6.6	7.14 4.87)	2.87	24.53	**0**	**26.78**	2.9	0.21
agonism	7.33	23.73	6.12	20.25	10.42 (6.77	6.09 3.59)	3.05	23.86	**1.56**	**21.10**	**1.91**	**5.74**
null	**0**	**26.19**	**0.71**	**10.38**	3.21 (2.8	6.07 30.28)	2.15	27.11	**0.59**	**24.69**	2.89 **(0**	0.27 **13.22)**

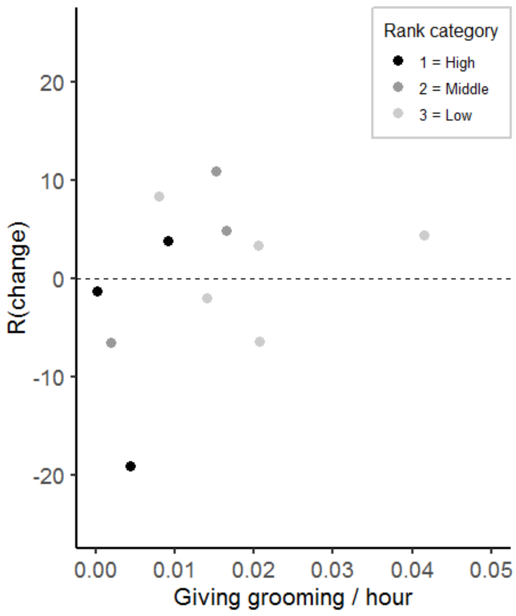


Figure 5.23 Males' resilience measured as R_{change} in relation to the rate of giving grooming [duration of grooming in hours/focal hour] (Δ AIC_C = 0 and R^2 = 15.03%).

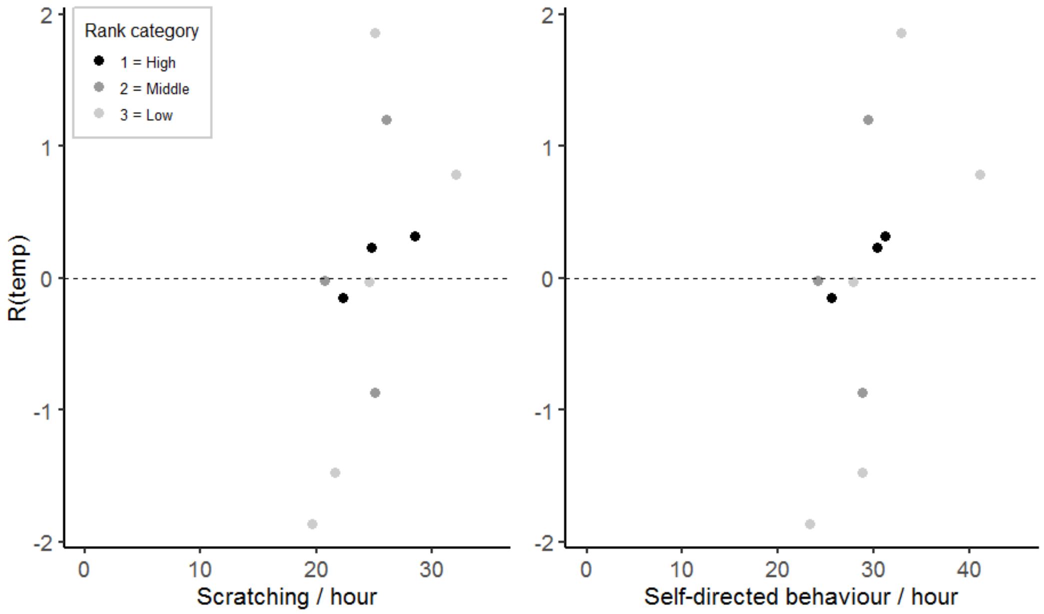


Figure 5.24 Males' resilience measured as R_{temp} in relation to the rate of scratching [count of scratching/focal hour] on the left and the rate of total self-directed behaviour [count of all self-directed behaviour/focal hour] on the right (scratching: Δ AIC_C = 0.95 and R^2 = 52.59%; self-directed behaviour: Δ AIC_C = 0 and R^2 = 55.99%).

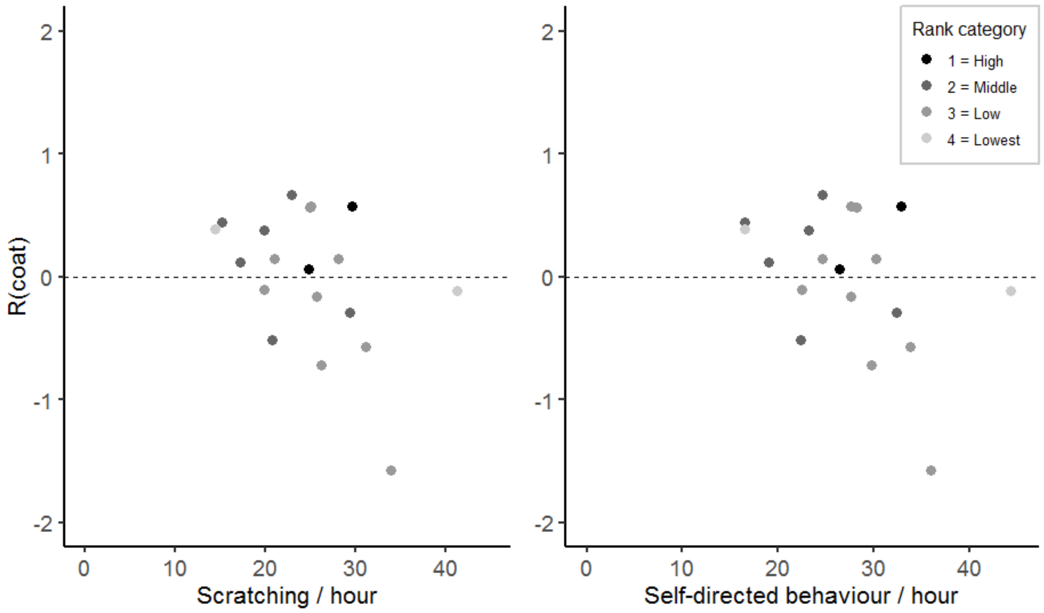


Figure 5.25 Females' resilience measured as R_{coat} in relation to the rate of scratching [count of scratching/focal hour] on the left and the rate of total self-directed behaviour [count of all self-directed behaviours/focal hour] on the right (scratching: Δ AIC_C = 0 and R^2 = 43.81%; self-directed behaviour: Δ AIC_C = 0.66 and R^2 = 42.02%).

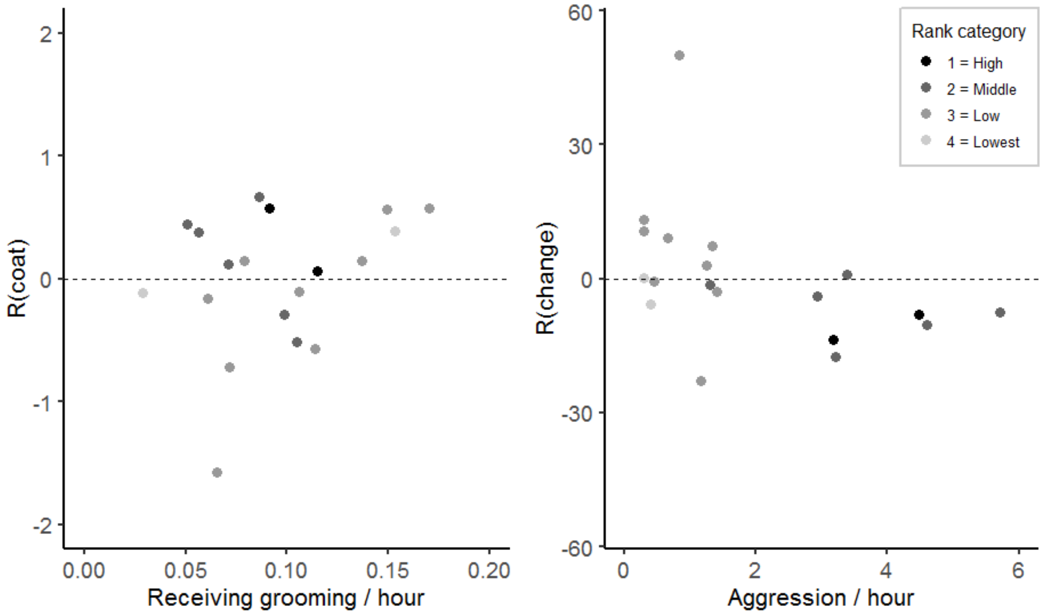


Figure 5.26 Females' resilience measured as R_{coat} in relation to the rate of receiving grooming [duration of grooming in hours/focal hour] on the left and their R_{change} in relation to the rate of aggression given [count of aggression/focal hour] on the right (receiving grooming: Δ AIC_C = 0.26 and R^2 = 43.11%; aggression: Δ AIC_C = 0 and R^2 = 26.78%).

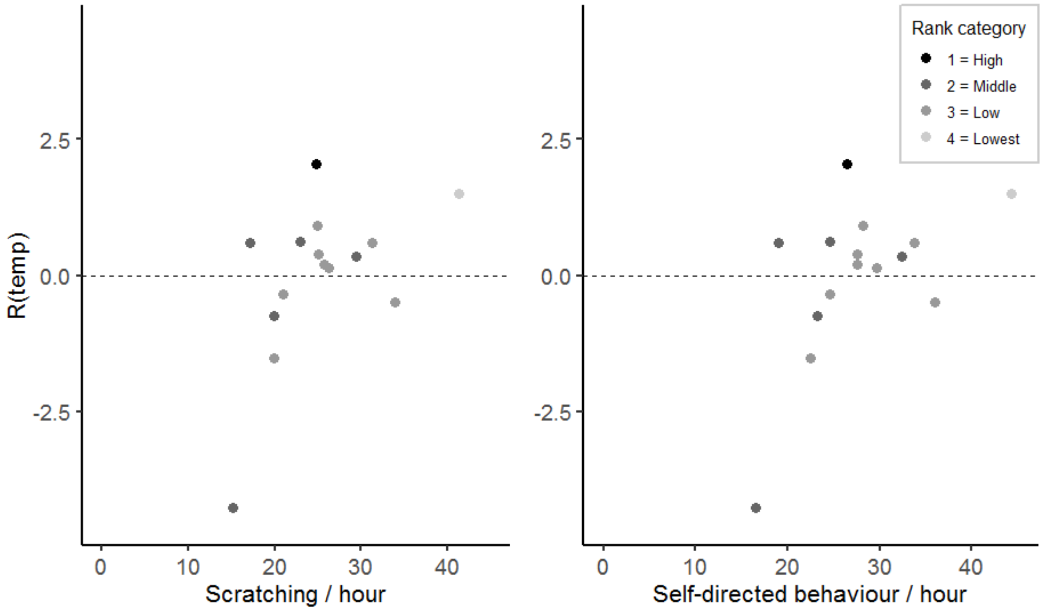


Figure 5.27 Females' resilience measured as R_{temp} in relation to the rate of scratching [count of scratching/focal hour] on the left and the rate of total self-directed behaviour [count of all self-directed behaviours/focal hour] on the right (scratching: Δ AIC_C = 0.65 and R^2 = 31.68%; self-directed behaviour: Δ AIC_C = 0 and R^2 = 34.17%).

Prediction 3ii: High resilience is linked to strong social bonds, reflecting social resilience.

LMs were constructed using measures of social bond strength to investigate variation in resilience. Fixed effects included in the full models were the sum of the top three CSI scores, the highest CSI score, the number of strong bonds an individual had (i.e. CSI > 1), and the number of weak bonds an individual had (i.e. CSI < 1), comparable to the analysis of social buffering in chapter 4. All models included age and rank category. Results of the model comparison are shown in Table 5.16 and details of the full models can be found in Appendix V-IV.

For males, none of the full models regarding R_{coat} or R_{change} received any substantial support. In the models investigating males' R_{temp}, though, there were influential data points in the full model including highest CSI score and in the full model including the number of strong bonds. Once the influential point in the latter model was removed (an adolescent male with no strong bonds), the full model including number of strong bonds was the best model and explained over 60% of variation compared to the just under 4% of variation explained by the null model. Here, males with more strong bonds had lower R_{temp} than males with fewer strong bonds (Figure 5.28).

For females, there were some problems with the assumptions of linear models regarding the models on R_{change} and R_{temp}, hinting at non-normal distributions of resilience measures, and potential non-linear relationships between predictor and response variables. While none of the full models received support based on AIC_C comparisons as all null models had the lowest AIC_C and all Δ AIC_C for other models were > 2, the full model including number of strong bonds of females' R_{temp} had an effect size 13% larger than the null model, and a Δ AIC_C just over 2. As for males, females with more strong bonds had lower R_{temp} than females with fewer strong bonds (Figure 5.28).

LM: *resilience measure ~ social bond measure + age class + rank category*

Table 5.16 Results of LM comparisons regarding the link between social bonds and measures of resilience (R_{coat}, R_{change}, and R_{temp}) of males and females. Models included age and rank category. Models with a Δ $AIC_C < 2$ or strikingly large effect sizes were considered to have received substantial support and are marked in bold and underlined. Numbers in brackets represent model comparison results once influential data points (Cook's distance > 1) were removed; if different full models had different individuals as influential data points, a new null model was calculated for each case and comparisons are marked by superscript numbers.

	MALES						FEMALES					
	Response variable: (Δ AIC_C, marginal R^2 [%])											
	R_{coat}		R_{change}		R_{temp}		R_{coat}		R_{change}		R_{temp}	
Predictor:	**Δ AIC_C**	**R^2**	**Δ AIC_C**	**R^2**	**Δ AIC_C**	**R^2**	**Δ AIC_C**	**R^2**	**Δ AIC_C**	**R^2**	**Δ AIC_C**	**R^2**
sum (top 3 CSI)	2.42	46.79	7.26	9.61	4	24.45	3.65	26.22	3.25	25.26	3.98	3.81
highest CSI	4.36	38.43	7.18	10.09	5.79 (8.7	14.54 11.57)^1	3.72	25.98	3.76	23.51	4.15	2.95
no. strong CSI (CSI > 1)	4.82	36.28	7.28	9.53	3.67 **(0**	26.19 **64.08)^2**	2.19	31.05	3.24	25.3	**2.06**	**13.20**
no. weak CSI (CSI < 1)	6.18	29.68	6.96	11.41	4.89	19.65	2.56	29.84	2.5	27.80	2.45	11.38
null model	**0**	**26.19**	**0**	**10.38**	**0** **(0** (3.56	**6.07** **11.12)^1** 3.50)^2	**0**	**27.11**	**0**	**24.69**	**0**	**0.27**

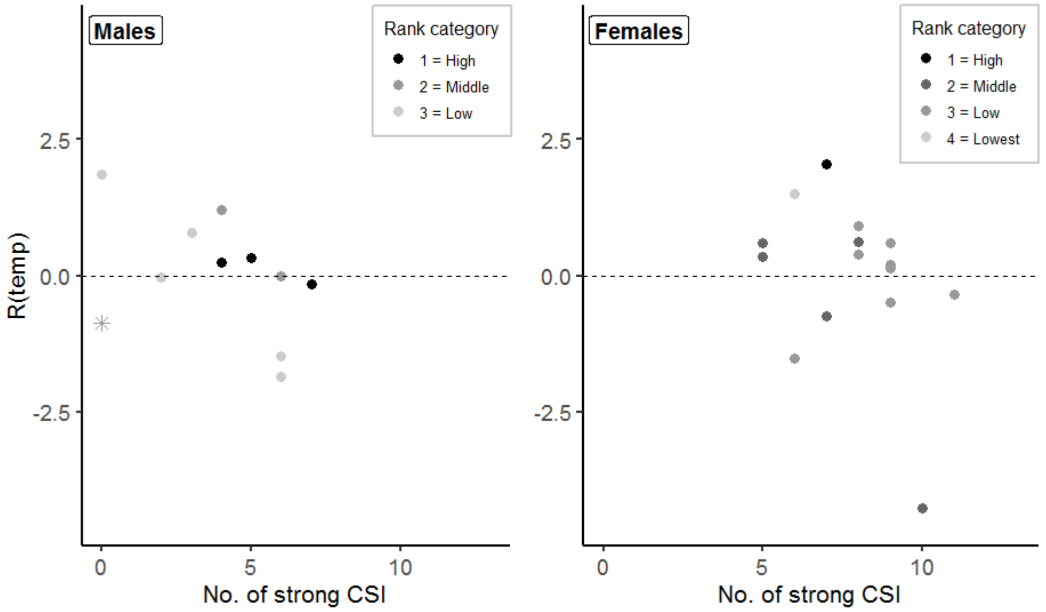


Figure 5.28 Males' (left) and females' (right) resilience measured as R_{temp} in relation to the number of strong social bonds, i.e. CSI > 1 (males, with influential data point (marked *): Δ $AIC_C = 3.67$ and $R^2 = 26.19\%$, without influential data point: Δ $AIC_C = 0$ and $R^2 = 64.08\%$; females: Δ $AIC_C = 2.06$ and $R^2 = 13.20\%$).

Prediction 3iii: High resilience is linked to high centrality in the affiliation network, reflecting social resilience.

To investigate whether centrality in an affiliative social network was linked to higher resilience, models were constructed using the social network measures calculated in chapter 4. Models also included age and rank. Full models were then compared to null models, and models that received substantial support either due to low AIC_C or due to exceptionally large effect sizes were subsequently investigated using a permutation approach, as described in detail in chapter 2. Only models whose estimates were significantly less frequent than estimates based on randomised models will finally be considered as meaningful. Results of model comparisons are given in Table 5.17 and results of permutation tests are shown in Table 5.18, while details of all models and the permutation procedure can be found in Appendix V-IV. The affiliative social network based on dyadic CSI values of all study subjects is shown in Figure 5.29.

For males, there was high multicollinearity between individual clustering coefficient and age, so age was excluded from these models. Based on the model comparison, models including strength, eigenvector centrality, and individual clustering coefficient received substantial support in explaining R_{coat} in males, besides the null model. While the Δ AIC_C values were larger than 2 for the strength and eigenvector centrality models, they explained an additional 20% of variation in this resilience measure compared to the null model and were therefore included in the permutation tests. The full models including clustering coefficients received substantial support in explaining males' R_{change} and R_{temp}, even after an influential data point was removed in the latter model. Regarding R_{temp}, the full model containing reach also received support, once an influential data point was removed (an adolescent male with very low reach).

However, the permutation procedure revealed that for these measures, none of the observed models differed significantly from random models (i.e. all $p > 0.05$, Table 5.18).

For females, there were some problems with linear model assumptions, hinting at non-normal distributions and non-linear relationships between predictors and response variables in the models of R_{change} and R_{temp}. Only the full models containing the individual clustering coefficient received substantial support in explaining R_{change} and R_{temp}, the latter again due to a higher effect size compared to the null model. Based on the permutation procedure, only the model including individual clustering coefficients investigating females' R_{change} was significantly different from random models ($p < 0.01$, Table 5.18). Here, females with a higher individual clustering coefficient, indicating higher cliquishness, had lower resilience than females which were less cliquish (Figure 5.30).

LM: *resilience measure ~ network metric + age class + rank category*

Table 5.17 Results of LM comparisons regarding the link between position in an affiliative social network based on dyadic CSI and resilience (R_{coat}, R_{change}, and R_{temp}) of males and females. Models included age and rank category. Models with a $\Delta AIC_C < 2$ or strikingly large effect sizes were considered to have received substantial support and are marked in bold and underlined. Numbers in brackets represent model comparison results once influential data points (Cook's distance > 1) were removed; if different full models had different individuals as influential data points, a new null model was calculated for each case and comparisons are marked by superscript numbers.

	MALES						FEMALES					
	Response variable: (ΔAIC_C, marginal R^2 [%])											
	R_{coat}		**R_{change}**		**R_{temp}**		**R_{coat}**		**R_{change}**		**R_{temp}**	
Predictor:	**ΔAIC_C**	**R^2**	**ΔAIC_C**	**R^2**	**ΔAIC_C**	**R^2**	**ΔAIC_C**	**R^2**	**ΔAIC_C**	**R^2**	**ΔAIC_C**	**R^2**
strength	**2.94**	**45.85**	16.8	9.55	8.97	29.83	3.56	26.55	6.62	24.72	4.66	0.30
eigenvector centrality	**2.38**	**48.11**	16.86	9.20	8.72	31.12	3.7	26.04	6.24	26.02	4.66	0.30
betweenness centrality	5.6	33.97	16.14	13.48	12.18	12.31	3.71	26.03	6.83	23.98	4.58	0.73
clustering coefficient	**0**	**22.88**	**0**	**4.85**	**0** **(0**	**16.81** **48.37)^1**	3.46	26.81	**0**	**44.83**	**2.34**	**11.9**
reach	5.22	35.78	16.86	9.20	11.47 **(0**	16.44 **63.03)^2**	3.13	27.99	6.72	24.37	3.7	5.24
null model	**0.23**	**26.19**	9.54	10.38	6.01 (8.31 (3.23	6.07 6.57)^1 3.50)^2	**0**	**27.11**	3.21	24.69	**0**	**0.27**

Table 5.18 Results of permutation tests regarding the link between network position in an affiliative network based on dyadic CSI and resilience (R_{coat}, R_{change}, and R_{temp}) of males and females. Models included age and rank category; a node permutation procedure was used with 1000 permutations. Permutation tests were based on results of the model comparisons in Table 5.17. Models with a p < 0.05 are marked in bold.

Sex	Resilience measure	Metric	Proportion observed est. < randomised est.	Proportion observed est. > randomised est.
MALES	R_{coat}	strength	0.07	0.93
		eigenvector centrality	0.08	0.92
		clustering coefficient	0.35	0.65
	R_{change}	clustering coefficient	0.49	0.51
	R_{temp}	clustering coefficient	0.62	0.38
		reach	0.70	0.30
FEMALES	**R_{change}**	**clustering coefficient**	**>0.99**	**<0.01**
	R_{temp}	clustering coefficient	0.07	0.93

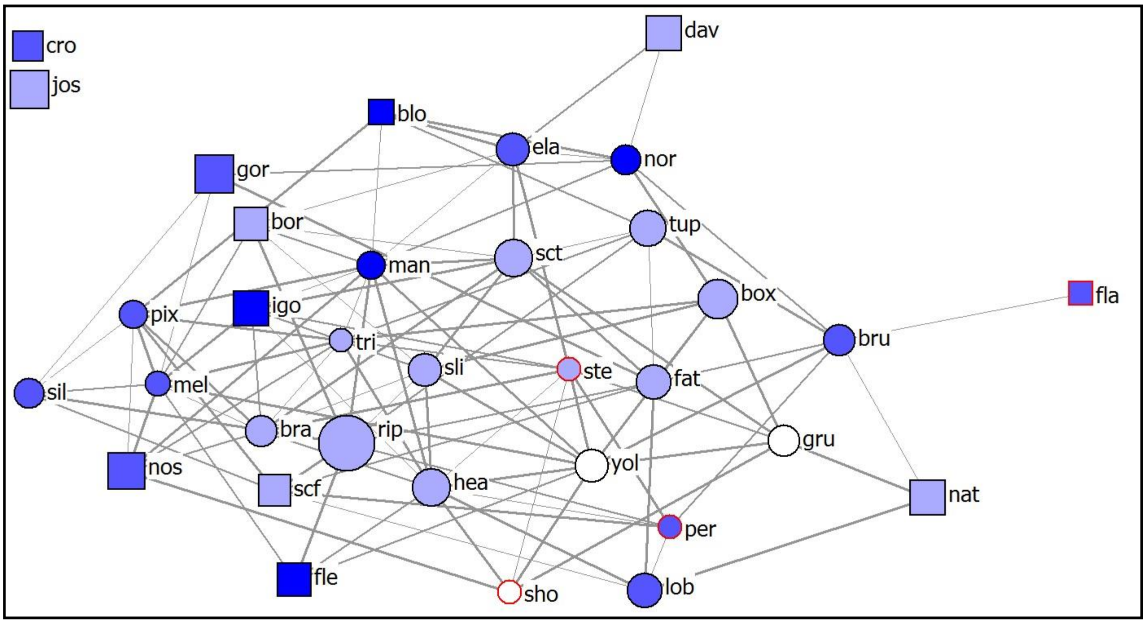


Figure 5.29 Undirected affiliative social network based on dyadic CSI values of all study subjects. Nodes represent individuals and edges represent dyadic CSI values above average (CSI > 1), with edge width reflecting bond strength. Node shape shows sex (squares = males, circles = females). Node size reflects the individuals' R_{change}, with larger nodes symbolizing higher resilience. Node colour represents rank category (darker = higher-ranking). R_{change} was not available for 4 individuals, which are marked by red rims around their nodes (fla, per, sho, ste), and which were not included in statistical models. Individual clustering coefficient was found to be negatively linked to R_{change} in females (=circles).

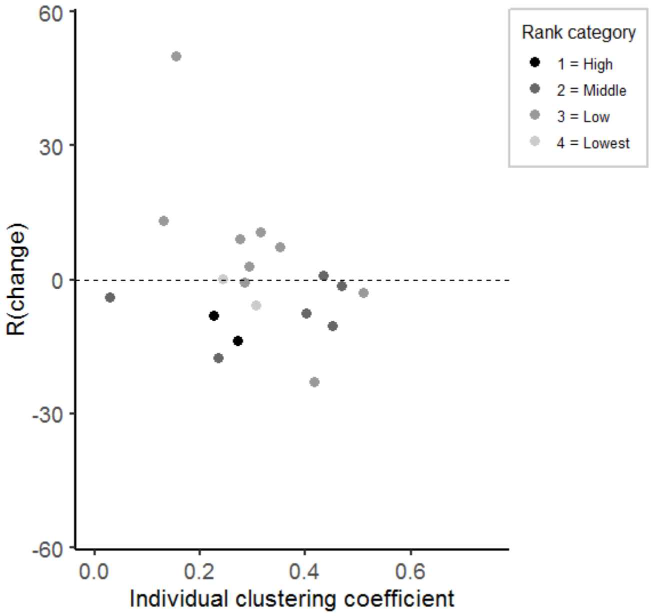


Figure 5.30 Females' R_{change} in relation to the individual clustering coefficient in an affiliative social network based on dyadic CSI (Δ AIC_C = 0 and R^2 = 44.83%, $p_{(Permutation)}$ < 0.01).

Prediction 3iv: High resilience is linked to high centrality in the agonism network, reflecting social resilience.

In addition to the affiliation network, it was also investigated whether position in an agonistic social network was connected to measures of resilience. In addition to the network metrics used under prediction 3iii, models using the degree in a network were also included. Results of model comparisons are compiled in Table 5.19, and based on these, permutation tests were conducted with results being shown in Table 5.20. Details on models and the permutation procedure can be found in Appendix V-IV. The undirected agonistic social network can be seen in relation to R_{temp} in Figure 5.31, and in relation to R_{coat} in Figure 5.32.

For males, there was generally high multicollinearity between degree in the agonism network and rank, so rank was excluded from all degree models. Regarding R_{coat}, only the full model including degree and the null model received substantial support with Δ AIC_C < 2. Regarding R_{change}, there was high multicollinearity between rank and betweenness centrality once an influential data point was removed, so rank was excluded here as well. Here, the full model including degree and the full model including betweenness centrality, after removing the influential data point, received substantial support with Δ $AIC_C < 2$, in addition to the null model, and were thus included in the permutation procedure. For models regarding R_{temp}, different individuals were influential data points in different models, so superscript numbers in the results table indicate which models were compared with each other. Once the influential data point was removed from the clustering coefficient model, there was high multicollinearity between rank and the clustering coefficients, so rank was excluded; when the influential data point in the betweenness model was removed, age was excluded due to high subsequent multicollinearity with betweenness. When also considering the models after influential data points were removed, full models including degree, clustering coefficient, and reach received substantial support in addition to the null model with all Δ $AIC_C < 2$. Based on the node permutation procedures, only the full model including reach explaining variation in males' R_{temp} was significantly different from random, with males with a higher reach having lower resilience (Figure 5.31, Figure 5.33).

For females, there were a few problems with model assumptions: regarding R_{coat}, in the model including reach as a fixed effect there was no homoscedasticity of residuals; regarding some R_{change} models, there was some evidence towards a non-linear relationship between predictor and response variables, as well as non-normal distribution of the response variable; and regarding R_{temp}, there was some indication as well that the response variable might not be normally distributed, and that there might be a non-linear relationship between the response variable and clustering coefficient as fixed effect. Only the full models including reach received substantial support in explaining variation in both R_{coat} and R_{change}, with them having the lowest AIC_C and explaining about 45% and 38% of variation, respectively. Regarding R_{temp}, there was high multicollinearity between rank and both strength and eigenvector centrality, so rank was excluded from the respective models. Subsequently, in addition to the null model, the full models including strength, eigenvector centrality, and betweenness centrality received substantial support with all $\Delta\ AIC_C < 2$, the latter explaining nearly 50% of variation after the removal of an influential data point. Furthermore, the degree model had an effect size of 39% after an influential data point was excluded and was therefore included in the permutation tests, even though $\Delta\ AIC_C = 2.93$. Based on the node permutation procedures, the full model including reach explaining variation in females' R_{coat} was significantly different from random, with females with high reach having higher resilience (Figure 5.32, Figure 5.34). Additionally, the full model including betweenness centrality was significantly different from random in explaining females' R_{temp}, with more central females being more resilient (Figure 5.31, Figure 5.34).

LM: *resilience measure ~ network metric + age class + rank category*

Table 5.19 Results of LM comparisons regarding the link between position in an agonistic social network and resilience (R_{coat}, R_{change}, and R_{temp}) of males and females. Models included age and rank category. Models with a Δ AIC_C < 2 or strikingly large effect sizes were considered to have received substantial support and are marked in bold and underlined. Numbers in brackets represent model comparison results once influential data points (Cook's distance > 1) were removed; if different full models had different individuals as influential data points, a new null model was calculated for each case and comparisons are marked by superscript numbers.

	MALES						FEMALES					
	Response variable: (Δ AIC_C, marginal R^2 [%])											
	R_{coat}		**R_{change}**		**R_{temp}**		**R_{coat}**		**R_{change}**		**R_{temp}**	
Predictor:	**Δ AIC_C**	**R^2**	**Δ AIC_C**	**R^2**	**Δ AIC_C**	**R^2**	**Δ AIC_C**	**R^2**	**Δ AIC_C**	**R^2**	**Δ AIC_C**	**R^2**
strength	7.01 (7.68	25.44 22.13)	6.98	11.32	8.53	14.98	4.85	30.45	3.77	26.12	**0**	**6.12**
degree	**0.32**	**24.32**	**0.16**	**9.32**	**1.18**	**16.91**	5.77	27.40	4.48	23.72	4.58 **(2.93**	6.06 **39.21)**
eigenvector centrality	7 (7.76	25.48 21.70)	6.47	14.29	9.64 (8.05	8.44 15.56)^1	5.36	28.76	4.52	23.52	**0.14**	**5.38**
betweenness centrality	7.21	24.38	5.87 **(0.19**	17.71 **9.50)**	9.99 (3.92	6.34 3.07)^2	6.06	26.44	2.85	29.2	3.08 **(0**	13.35 **49.34)**
clustering coefficient	5.05	34.35	7.33	9.23	10.15 **(0.6**	5.35 **6.75)^1**	6.21	25.91	4.47	23.7	5.64	0.64
reach	5.47 (8.8	33.23 15.54)	6.67	13.12	**0**	**56.63**	**0**	**44.67**	**0** (3.21	**38.05** 20.05)	5.24	2.75
null model	**0** **(0**	**26.19** **16.33)**	**0** **(0**	**10.38** **10.86)**	2.82 **(0** **(0**	6.07 **11.12)^1** **30.28)^2**	2.47	27.11	**0.77** **(0**	**24.69** **18.28)**	**1.05** (4.09	**0.27** 13.22)

Table 5.20 Results of permutation tests regarding the link between network position in an agonistic network and resilience (R_{coat}, R_{change}, and R_{temp}) of males and females. Models included age and rank category; a node permutation procedure was used with 1000 permutations. Permutation tests were based on results of the model comparisons in Table 5.19. Models with a p < .05 are marked in bold.

Sex	**Resilience measure**	**Metric**	**Proportion observed est. < randomised est.**	**Proportion observed est. > randomised est.**
MALES	R_{coat}	degree	0.15	0.85
	R_{change}	degree	0.71	0.19
		betweenness centrality	0.13	0.87
	R_{temp}	degree	0.87	0.13
		clustering coefficient	0.50	0.50
		reach	**1.00**	**0.00**
FEMALES	**R_{coat}**	**reach**	**0.02**	**0.98**
	R_{change}	reach	0.95	0.05
	R_{temp}	strength	0.14	0.86
		degree	0.07	0.93
		eigenvector centrality	0.06	0.94
		betweenness centrality	**0.03**	**0.97**

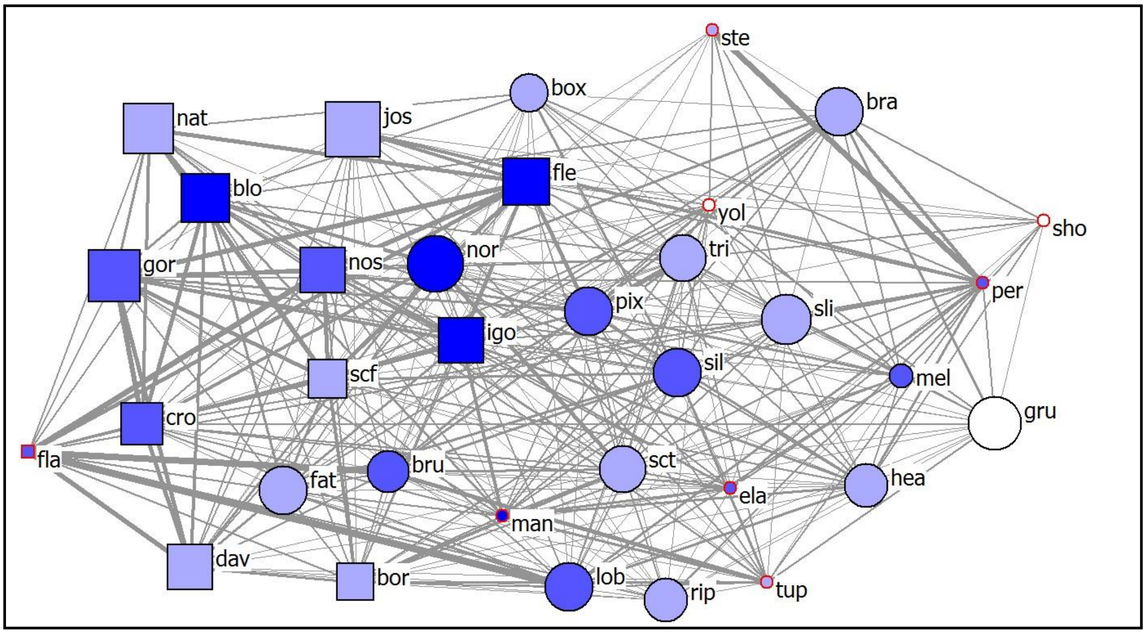


Figure 5.31 Undirected social network based on agonistic behaviour of all study subjects. Nodes represent individuals and edge widths represent the rate of any kind of agonistic (i.e. aggressive or submissive) behaviour. Node shape shows sex (squares = males, circles = females). Node size reflects the individuals' R_{temp}, with larger nodes symbolizing a higher resilience. Node colour represents rank category (darker = higher-ranking). R_{temp} values were not available for 8 individuals, which are marked by red rims around their nodes (ela, fla, man, per, sho, ste, tup, yol), and which were not included in statistical models. For males (=squares), reach was negatively linked to R_{temp}, while for females (=circles) betweenness centrality was positively linked to R_{temp}, i.e. for males, high connectedness was linked to lower resilience, while for females, centrality was connected to higher resilience.

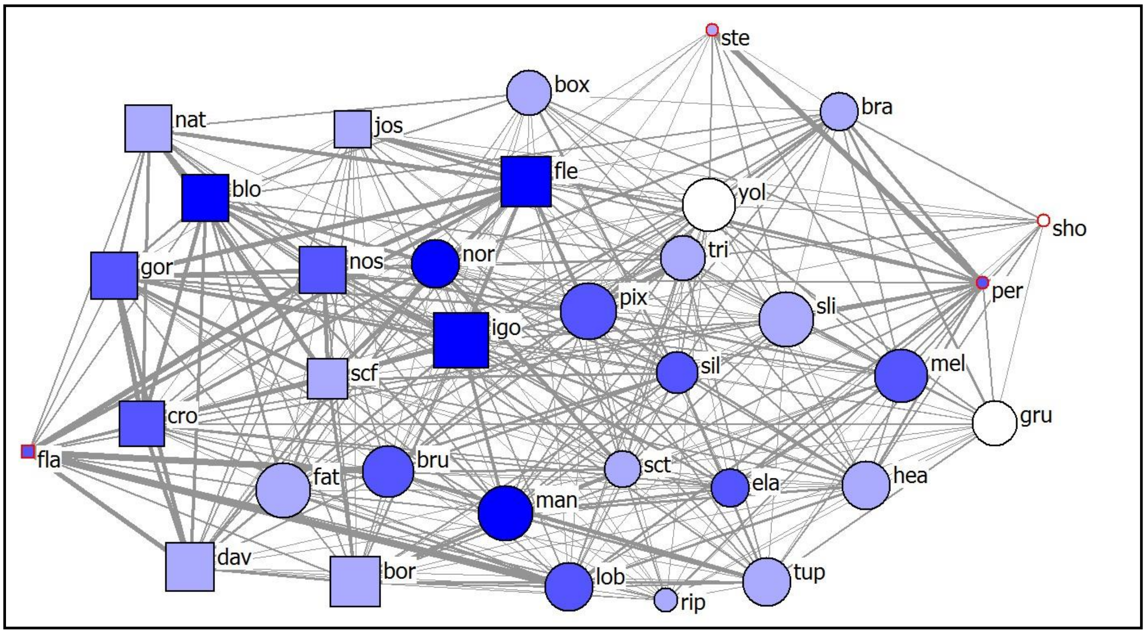


Figure 5.32 Undirected social network based on agonistic behaviour of all study subjects. Nodes represent individuals and edge widths represent the rate of any kind of agonistic (i.e. aggressive or submissive) behaviour. Node shape shows sex (squares = males, circles = females). Node size reflects the individuals' R_{coat}, with larger nodes symbolizing a higher resilience. Node colour represents rank category (darker = higher-ranking). R_{coat} values were not available for 4 individuals, which are marked by red rims around their nodes (fla, per, sho, ste), and which were not included in statistical models. For females (=circles), reach was positively linked to R_{coat}, i.e. females with high connectedness had higher resilience.

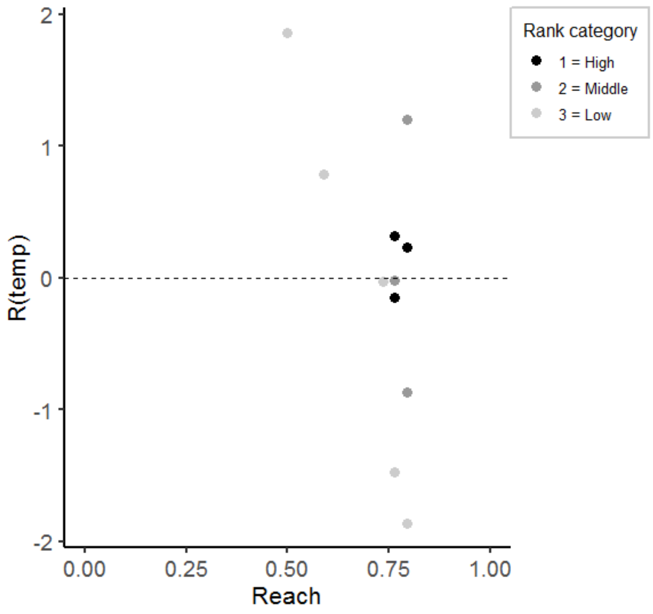


Figure 5.33 Males' R$_{temp}$ in relation to reach in an agonistic social network (Δ AICc = 0 and R^2 = 54.63%, p$_{(Permutation)}$ = 0.00).

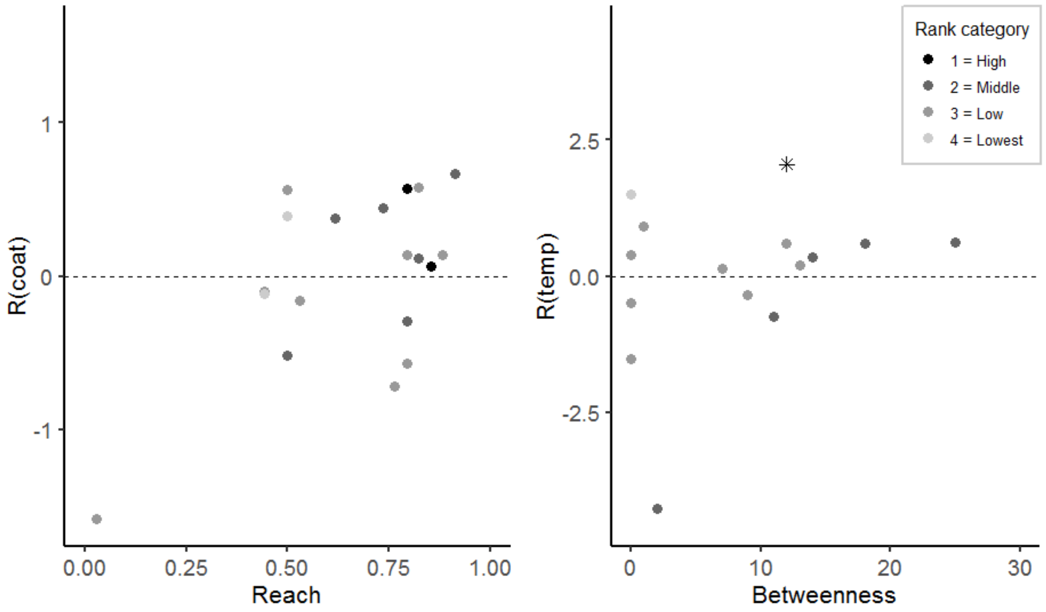


Figure 5.34 Females' R$_{coat}$ in relation to reach (left) and females' R$_{temp}$ in relation to betweenness centrality (right) in an agonistic social network (R$_{coat}$: Δ AICc = 0 and R^2 = 44.67%, p$_{(Permutation)}$ < .02; R$_{temp}$, with influential data point (marked *): Δ AICc = 3.08 and R^2 = 13.35%, p$_{(Permutation)}$ = .03, without influential data point: Δ AICc = 0 and R^2 = 49.34%).

5.4.4 Summary

To summarise, the three measures of resilience developed and investigated in the context of this study were linked to different demographic, reproductive, and social or behavioural factors (for an overview of results see Table 5.21). There were no overall differences in resilience measures between the sexes. While there was not much variation in males' R_{coat}, females R_{coat} decreased with older age and was positively linked to higher rank, as well as to the number of surviving infants, and was generally higher in females who did not lose an infant in the last three years compared to females who did. Furthermore, females' R_{coat} was negatively linked to rates of scratching and all self-directed behaviours, positively linked to rates of receiving grooming, and also positively linked to having a large network, measured as reach, in the agonism network. In contrast, females' R_{change} was negatively linked to dominance rank position, in that lower ranking females had higher R_{change}. Additionally, R_{change} varied with reproduction, i.e. females with more surviving infants had lower R_{change}, and decreased with increasing clustering coefficient in the affiliative network for females. For males, R_{change} was positively linked to rates of giving grooming but unrelated to any other of the explored variables. Finally, R_{temp} was in both sexes strongly positively linked to rates of self-directed behaviour and scratching. There was also some evidence that both males and females had lower R_{temp} the more strong bonds (CSI > 1) they had. Additionally, in females higher R_{temp} was linked to lower mean fGCM concentrations and high centrality in the agonism network, measured as betweenness centrality, while in males it was positively associated with having a smaller network, i.e. lower reach, in the agonism network.

Table 5.21 Summary of the results of chapter 5, investigating whether measures of resilience (R_{coat}, R_{change}, and R_{temp}) are linked to demographic factors such as age and dominance rank position; whether they are linked to mean fGCM levels and reproductive output in females; and investigating whether resilience was behaviourally or socially mediated, i.e. whether high resilience was linked to high rates of potential coping behaviours, strong social bonds, or centrality in an affiliative or an agonistic social network. Findings supporting predictions are marked by a grey background; direction of estimates of fixed effects in LMs are indicated by ↓ for negative prediction and ↑ for positive prediction (♀ = female, ♂ = male, ns = not significant, SDB = all self-directed behaviours, SR = scratching, AG = agonism, AGGR = aggression, GR = grooming).

Hypothesis 1: Measures of resilience are linked to demographic factors.			
	R_{coat}	**R_{change}**	**R_{temp}**
Resilience decreases with age	♀ (in LM: ↓) ♂ ns	♀ ns ♂ ns	♀ ns ♂ ns
Higher resilience with higher rank	♀ rank category & rand. Elo-rating: ↑ ♂ ns	♀ rank category & rand. Elo-rating: ↓ ♂ ns	♀ ns ♂ ns
Hypothesis 2: Resilience is linked to reproduction and mean physiological stress response levels.			
	R_{coat}	**R_{change}**	**R_{temp}**
Low resilience ~ high mean fGCM concentrations	♀ ns ♂ ns	♀ ns ♂ ns	♀ ↓ ♂ ns
Lactating females have lower resilience	lactation: ns [nr. of surviving inf: ↑]	lactation: ns [nr. of surviving inf: ↓]	lactation: ns [nr. of surviving inf: ns]
Females that lost an infant have lower resilience	lost an infant: ↓	lost an infant: ns	lost an infant: ns
Hypothesis 3: Resilience is behaviourally or socially mediated.			
	R_{coat}	**R_{change}**	**R_{temp}**
Resilience positively predicted by			
long-term rates of behaviour	♀ SR & SDB: ↓ GR received: ↑ ♂ ns	♀ AGGR & AG: ↓ [probably a rank effect] ♂ GR given: ↑	♀ SR & SDB: ↑ ♂ SR & SDB: ↑
social bonds	♀ ns ♂ ns	♀ ns ♂ ns	♀ no. strong CSI ↓ ♂ no. strong CSI ↓
centrality in affiliation network	♀ ns ♂ ns	♀ clustering coefficient ↓ ♂ ns	♀ ns ♂ ns
centrality in agonism network	♀ reach ↑ ♂ ns	♀ ns ♂ ns	♀ betweenness centr. ↑ ♂ reach ↓

5.5 Discussion

The aim of this chapter was to develop measures of resilience that can be used practically in the study of wild non-human primates. To this end, I explored IRT as a new tool to assess coat quality quantitatively. The newly developed IRT measure *delta coat* *temperature* was, in combination with two measures of coat condition based on observer ratings, used to calculate resilience as the residuals of linear models using demonstrated reactive scope as the predictor variable and coat condition measures as response variables. Using the resulting three original measures of resilience – R_{coat}, R_{change}, and R_{temp} – it was investigated whether these were linked to demographic and reproductive factors as well as mean physiological stress response levels. I found strong evidence that resilience in chacma baboons might be behaviourally mediated, and limited evidence for social mediation of resilience.

5.5.1 Developing a measure of resilience

5.5.1.1 Exploration of infrared thermography and coat condition measures

The first part of this chapter was of an explorative nature, investigating the use of IRT in wild non-human primates and developing different measures of resilience. Regarding the first part, only one other study has yet used IRT to assess coat temperatures in a wild non-human primate species, i.e. in mantled howling monkeys (*Alouatta palliata*; Thompson et al., 2017b), while IRT has been used in chimpanzees (*Pan troglodytes*) to investigate skin temperature of the swelling in different reproductive states (Dezecache et al., 2017a) and changes in skin temperature of the nose and ear in response to conspecifics‘ vocalizations (Dezecache et al., 2017b). The current study is the first to utilise infrared measurements to assess coat condition quantitatively and develop a new measurement for that purpose. This measurement, i.e. *delta coat temperature* which is measured as the difference between maximum and minimum coat temperature measured on the side of the trunk, was found not to be affected by any measure of ambient temperature, humidity or windspeed, and was also not directly linked to maximal abdominal skin temperature or average coat temperature, which themselves were found to be affected by weather conditions. Additionally, there was marked inter-individual variation in delta coat temperature, making it an ideal candidate for the quantitative assessment of coat condition. In the context of this study, it was not possible or necessary to verify whether measured temperatures precisely reflected actual coat temperatures, as only the difference between maximal and minimal coat temperatures was of interest, this difference taken to reflect the degree of uniformity or homogeneity of the coat.

Before calculating measures of resilience, I explored how coat condition ratings linked to reproductive status, and how the three measures of coat condition, i.e. average coat condition, relative change in coat condition, and delta coat temperature, were linked to age and rank, as significant effects of these demographic factors on coat condition might subsequently explain observed differences in resilience measures. Firstly, lactating and pregnant females had better coat condition ratings than cycling females. This is in contrast to a previous study on ring-tailed lemurs (*Lemur catta*), which found that lactating females had a stronger decline in coat condition over the dry season than non-lactating females (Jolly, 2009), and indicates that lactating and carrying an infant does not in itself lead to a worse coat condition. Regarding age, there was weak evidence from linear models that older females had worse average coat condition than younger females. Additionally, higher rank was linked to better average coat condition in males and females, which is in line with findings in captive female rhesus macaques (*Macaca mulatta*; Beisner and Isbell, 2009), but surprisingly high-ranking females, while having overall better coat condition, had worse development of their coat condition over the dry season than low-ranking females. While it would have also been very interesting to investigate how specific events such as predation or parturition affect coat condition, this was not possible here due to the limited duration of the study and due to coat condition ratings only being conducted during the dry season. Thus, individuals were only rated once before the first predation event and therefore a pre-/post-predation comparison was not possible.

5.5.1.2 Deriving measures of resilience

Using this new infrared measure as well as the two measures of coat condition based on more conventional scoring by observers, I subsequently developed a mathematical approach to assessing resilience non-invasively. For this purpose, linear models were constructed using average coat condition, the relative change of coat condition over the dry season, or delta coat temperature as response variables, and demonstrated reactive scope (DRS or DRS_{CV}) of fGCM levels as predictor. Resilience was then assessed as the residuals between observed and predicted values of coat condition. As resilience measures based on DRS and DRS_{CV} were highly correlated, only the resilience measures based on the three coat condition scores in relation to DRS_{CV} were further investigated (subsequently termed R_{coat}, R_{change}, and R_{temp}).

These three resilience measures, however, were not correlated with each other, suggesting that they might reflect different aspects of an individual's resilience. Specifically, R_{coat} was proposed to reflect the individual's general condition and thus longer-term resilience to adversities (such as environmental or social stressors), while R_{change} might indicate the individual's shorter-term resilience and connected ability to cope with the challenges of the dry season or any adversities they experienced during the dry season, such as predation events. R_{temp}, finally, was suggested to represent the individuals' resilience at the end of the study period, and thus also at the end of the dry season, and thus presents a cumulative measure of their coping success. This framework was supported by the results of the following analyses, as different factors linked to the three measures of resilience in different ways.

This is the first study that attempts to assess resilience in a wild primate population in an integrative manner, i.e. based on evolutionarily relevant measurements of success in dealing with everyday stressors, as well as on physiological mediators. Only a few studies have yet investigated hypotheses linked to the concept of resilience in wild non-human primates, and these considered reproductive resilience in response to environmental variation (e.g. in mouse lemurs [*Microcebus murinus*; Canale et al., 2012]), or explored the effect of early-life adversity on growth (Assamese macaques [*Macaca assamensis*; Berghänel et al., 2016]), reproductive resilience (yellow baboons [*Papio cynocephalus*; Lea et al., 2015]) or longevity (yellow baboons; Tung et al., 2016; Zipple et al., 2019). In contrast, this study acknowledges that individuals do differ in their neuroendocrine system, for example due to pre- and postnatal environments, genetic and epigenetic factors, as well as later-in-life coping experiences, and that they also differ in their current social, and to a certain degree ecological, environments, even while living in the same troop. Based on these differences, it was thus investigated whether individuals fared ‘better’ or ‘worse’ than expected for the range of physiological mediator utilised and relative to their conspecifics. This represents a novel approach to the study of inter-individual differences in wild primates.

5.5.2 Investigating resilience

5.5.2.1 Demographic factors

Hypothesis 1: Measures of resilience are linked to demographic factors.

Prediction 1i: Resilience decreases with age.

As a basis for the investigation into the proposed measures of resilience, it was first investigated whether resilience was linked to demographic factors such as age and dominance rank position. Regarding age, it was predicted that resilience would decrease with older age. In humans it is known that the factors connected to resilience change over the lifetime, so that resilience becomes more about the maintenance of abilities and less about coping with severe stressors (Clark et al., 2011). Here, while means of resilience measures did not significantly differ between age categories, there was some evidence that the resilience measure R_{coat} was lower in older females than in young adult females in accordance with the prediction, i.e. older females had worse condition coats than expected based on their physiological measure of stress reactivity. However, there was no difference between age classes in any other resilience measures for females and in males no evidence of variation in resilience across age classes for any of the three measures explored.

This finding fits with the proposed idea of R_{coat} representing the overall state of the individual. This decrease in resilience could theoretically be explained by age-related changes in HPA-axis functioning, based on either the allostasis or reactive scope models. The allostasis model proposes that physiological responses to stressors come with a cost to the systems, especially in the case of hyperreactivity or dysregulation, called 'wear and tear', and that these costs can accumulate over time, leading to increasing allostatic load (McEwen, 2003; Romero and Wingfield, 2015). Similarly, in the reactive scope model, repeated increases in the mediator can lead to a reduction of the threshold to homeostatic overload (Romero and Wingfield, 2015). In both cases, the range of mediator left to cope with further stressors would be narrowed, leaving a diminished flexibility to deal with subsequent stressors. While some studies have, in line with this logic, found increased rates of fGCM concentrations in old females, e.g. in grey mouse lemurs (*Microcebus murinus*) where heightened fGCM levels were interpreted as reduced coping ability (Hämäläinen et al., 2015), no clear patterns in age-related changes in physiological stress response measures across species have yet been found (as reviewed in Hämäläinen et al., 2015). Indeed, in the current study, old females had lower mean fGCM concentrations than middle-aged females, as described in chapter 3. Thus, the reduced R_{coat} of old females does not seem to be directly linked to heightened GC concentrations, but this does not exclude the possibility of repeated stressors over many years having a cumulative effect on HPA-axis function, with this in turn causing decreased resilience.

It should, however, also be considered that resilience might not be directly mediated by GC concentrations but might be linked to other physiological or psychological processes. As described above, in humans it was proposed that resilience in older age is more about the preservation of abilities and less about coping with severe adversities (Clark et al., 2011). Additionally, social support for example has been linked to psychological resilience in humans, but with older age the support network tends to shrink in humans (Clark et al., 2011). While it is unknown if and how social support affects resilience in animals, the social network of individuals changes over their lifetime as they lose bonded partners over time, and daughters for example become important social partners instead of the individual's mother (Japanese macaques [*Macaca fuscata*; MacDonald Pavelka, 1994]). These changes in social bonds could in turn affect resilience. Furthermore, resilience has recently received increased attention in biomedical research, where studies explore the use of mice models of age-related changes in resilience (Schosserer et al., 2019). It was found, for example, that frailty, which is defined as an accumulation of deficits and which has been linked to decreased resilience (Schosserer et al., 2019), increases with age in female mice and that it predicts mortality (Kwak et al., 2019). It is unknown, though, whether wild animals reach an age where the concept of frailty becomes relevant.

Alternatively, it also needs to be considered that older age might generally be linked to lower average coat condition. While alopecia has been observed to increase in older individuals (e.g. in captive female rhesus macaques [*Macaca mulatta*; Beisner and Isbell, 2009]), the females of the study troop did not suffer from alopecia, and there was only weak evidence for a worsening of average coat condition with older age.

There were no differences found in resilience between age classes in males. This might be due to a shorter lifespan in males than females (yellow baboons [*Papio cynocephalus*; Bronikowski et al., 2011]), although whether such a difference occurs in the study troop is unknown. It might also be due to worse health or general condition in old females compared to old males, or due to both longer lifespan and worse condition in old females, as is described in many human societies (the so-called 'health-survival-paradox', where women suffer more illnesses but also live longer; Alberts et al., 2014). Independent of the mechanism, the results supported the prediction of resilience decreasing with age in females, at least for resilience measured as R_{coat}.

Prediction 1ii: High-ranking individuals are more resilient than low-ranking individuals.

It was predicted that resilience would increase with increasing dominance rank, as higher rank is generally assumed to be beneficial, due to it often being connected to the availability of social support, and access to food and mating opportunities (Majolo et al., 2012). In contrast to this prediction, females' resilience, measured as R_{change}, decreased with increasing rank; all but one female of the two highest rank categories had negative R_{change} scores, while there was higher variability within the two lower rank categories. Females' R_{coat} or R_{temp} did not differ with dominance rank position, and there were no differences by rank in any of the three measures of resilience for males.

While these results are in contrast to the prediction, they do fit with the findings of chapter 3: there, females of the two high rank categories were found to have significantly higher mean fGCM concentrations than females of the two lower rank categories, suggesting that these females were more 'stressed', or that they had higher energetic demands during the study period, or that both of these things were the case. As R_{change} was proposed to reflect the ability to cope with the challenges connected to the dry season, such as low food availability, high fGCM levels could mean that high-ranking females needed to expend more energy to fulfil their energetic demands, or that they had generally higher baseline GC concentrations. The result that almost all high-ranking females had negative R_{change} suggests that they could not meet the energetic demands during the dry season and thus experienced decreases or smaller increases in coat condition than expected for their demonstrated reactive scope. For males, there was no link between rank category and any of the three resilience measures. Males also did not differ in mean fGCM concentrations by rank category, so this lack of link between rank and resilience fits the proposed explanation of the findings in females.

5.5.2.2 Reproduction and mean physiological stress response levels

Hypothesis 2: Resilience is linked to reproduction and mean physiological stress response levels.

Prediction 2i: Individuals with lower resilience have higher mean fGCM concentrations.

It was predicted that individuals that had higher mean fGCM concentrations would have lower resilience, based on the idea of 'wear and tear' connected to high levels of GC. While there was no link between mean fGCM concentrations and resilience in males, for females high mean fGCM levels were connected to lower resilience, measured as R_{temp}.

There are three potential explanations for this negative link between mean fGCM concentrations and resilience: firstly, heightened GC concentrations might be the cause of low resilience; secondly, low resilience might be the cause of high levels of GC; or lastly, high GC concentrations might reflect low resilience without being causally linked.

Regarding the first possibility of high levels of GC as a cause of low resilience, it has been repeatedly shown across vertebrate taxa that chronically increased levels of GC are linked to pathological outcomes, for example in cardiovascular, metabolic, reproductive, digestive, or immune processes (reviewed in Sapolsky, 2004; Nelson, 2005). While it has been questioned whether individuals of a natural population in a relatively undisturbed habitat experience chronic stress, a recent study showed that even transient spikes in GC can lead to increased GC concentrations in the longer term if the recovery time between stressors is insufficient (tree swallows [*Tachycineta bicolor*;

Taff et al., 2018]). As such, even short but frequent stressors could lead to chronically elevated GC concentrations and pathologies. Accordingly, in the reactive scope model, heightened levels of a mediator can lead to a decrease of the threshold to homeostatic overload, which leaves a smaller range of mediator to deal with subsequent stressors, which can be interpreted as decreased resilience.

The second possibility is that less resilient individuals have higher mean fGCM concentrations because of their low resilience. Here, less resilient animals might be more reactive to environmental stimuli or might need to mount a stronger physiological response to cope with adverse situations than more resilient individuals, which could lead to them having higher mean fGCM concentrations in the longer term. This interpretation would be in line with the 'for better or for worse' model, which posits that more reactive individuals will be more sensitive to beneficial stimuli but also be more reactive or susceptible to adverse situations, which could be linked to lower resilience, while less reactive individuals might not be as susceptible to either adverse or beneficial stimuli (Daskalakis et al., 2013).

The last possibility is that a high mean fGCM concentration reflects – but is not caused by, or a cause of – low resilience. Here, a robust GC response and an efficient termination via negative feedback are assumed to play an important role in mediating resilience. As such, resilient individuals would be able to mount an appropriate GC response but use a quick termination process to reduce the amount of energy needed to cope with the adversity and thus keep 'wear and tear' down to a minimum. An efficient negative feedback system was, for example, linked to a higher survival probability during starvation in Galapagos marine iguanas (*Amblyrhynchus cristatus*; Romero, 2012), and to higher reproductive success in tree swallows (*Tachycineta* *bicolor*; Vitousek et al., 2019). Less resilient individuals would experience higher or prolonged levels of GC, potentially due to a less effective negative feedback system. In that way, high GC concentrations are neither cause nor consequence of low resilience but rather a symptom of it.

Overall, the results of this study do not allow firm conclusions to be drawn regarding the mechanisms by which fGCM concentrations link to resilience. Additionally, the full model including mean fGCM concentrations only explained about 15% of variation in females' R_{temp}, which indicates that other factors might play a more important role in its mediation.

Prediction 2ii and 2iii: Females that were lactating during the study period or that lost an infant in the last three years have lower resilience.

It was predicted that females that were lactating during the study period or that had more surviving infants in the last three years would have lower resilience, and that females that lost an infant in the last three years would also have lower resilience. Indeed, the number of surviving infants a female had in the last three years was linked to resilience, i.e. females with a higher number of surviving infants had higher R_{coat} but lower R_{change}, and also the loss of an infant was associated with lower resilience, in that females who lost at least one infant in the last three years had lower R_{coat} than females who did not.

The predictions tested here were based on the assumption that females need to navigate a trade-off between costly reproduction and other energetic demands, such as immune function, as described above. Therefore, it was expected that females that were lactating would need to use a substantial part of their energy for maternal care and would have therefore less energy left for other functions, and that therefore, in the longer term, having many surviving infants might be connected to lower resilience as well. Similarly, it was expected that females that lost an infant would experience this as a major adverse event, which could lead to chronically or temporarily raised GC concentrations and thus to decreased resilience, or that losing an infant might reflect low resilience and the inability to successfully navigate this energetic trade-off. Indeed, both the number of surviving infants and the loss of an infant were linked to resilience.

Females that had two surviving infants had high R_{coat}, while all females with no surviving infants had a negative R_{coat}. This indicates that in the longer term, reproduction does not necessarily come with a cost to the overall condition of the female, as females with two surviving infants had better average coat condition relative to their DRS_{CV} than was predicted. Instead, females with high R_{coat} produced more offspring with an apparently higher survival probability, whereas females of worse condition than predicted based on their DRS_{CV} lost all of their offspring in these three years or did not give birth in the first place. As such, R_{coat} seems to well reflect females' ability to reproduce successfully. In line with these findings, females who lost at least one infant in the last three years had worse R_{coat} than females who did not lose any infants. With the data available in this study, it was not possible to ascertain, though, whether females had worse than expected coat condition because of the loss, or whether they had low resilience and were therefore not able to successfully care for their infant.

The association between R_{change} and the number of surviving infants was in the opposite direction. Here, females with two surviving infants had negative R_{change} (i.e. a worse development of coat condition over the dry season than predicted for their DRS_{CV}, which indicates a diminished ability to cope with the adversities connected to this season), while there was higher variability centring around zero for females with one surviving infant or none. While the lower R_{change} of females with more offspring could also reflect the current reproductive state, an exploratory analysis in the beginning showed that lactation and carrying of infants was not generally linked to lower coat condition, thus making it unlikely that the worse than based on their DRS_{CV} predicted development of coat condition was directly reflective of the current reproductive state. These results indicate that, while R_{coat} might reflect cumulative demands affecting resilience which in turn affects the ability to reproduce successfully, reproducing still comes with a cost or energetic trade-off, at least in the shorter term; this cost is reflected in the negative R_{change}.

5.5.2.3 Social and behavioural mediation of resilience

Hypothesis 3: Resilience is behaviourally or socially mediated.

> **Prediction 3i:** High resilience is linked to high rates of self-directed/affiliative/ agonistic behaviour, reflecting behavioural resilience.

It was predicted that high rates of potential coping behaviours would be linked to higher resilience, reflecting behaviourally mediated resilience. Indeed, results indicate that in both sexes R_{temp} was positively related to rates of scratching and other self-directed behaviours, and rates of giving grooming were also positively linked to R_{change} in males. For females, individuals that received grooming at high rates had high R_{coat}, while females that scratched or showed other self-directed behaviours at high rates had worse R_{coat}. Rates of aggression and agonism were negatively linked to R_{change} in females. In the following sections, first results that are in line with the prediction and then results that are contrary to the prediction, and alternative interpretations of these results, will be discussed.

Concerning R_{temp}, the results strongly support the prediction that resilience is behaviourally mediated. For both males and females, high rates of scratching and total self-directed behaviour were linked to higher R_{temp}. These results cannot be explained by directed manipulation of the fur through the scratching as then, if anything, scratching and self-grooming should lead to more irregularities in the fur and thus higher delta coat temperature than predicted given the DRS_{CV}, but instead high rates of scratching and self-directed behaviours were linked to lower than expected delta coat temperatures given the DRS_{CV}, thus a more homogeneous coat. Furthermore, these results fit the findings of chapter 4, which proposed that both males and females use these displacement behaviours to cope with adverse situations. There, it was found that males and females showed short-term increases in scratching and all self-directed behaviour in response to baiting (and predation in the case of females). In line with this finding, a study in rats (*Rattus norvegicus domestica*) found that the option to perform displacement behaviours during tail-shock experiments was linked to reduced behavioural measures of anxiety, which was interpreted as behavioural resilience (Helmreich et al., 2012). So overall, chapter 4 provided evidence that chacma baboons use displacement behaviours to cope with stress- or anxiety-inducing situations, and the current chapter adds evidence that these displacement behaviours might mediate resilience more generally.

Also in line with the prediction, there was support in males for resilience, measured as R_{change}, being mediated by their rates of giving grooming. Chapter 4 provided evidence that (low-ranking) males might use grooming as a coping behaviour, and accordingly, here males that showed higher rates of giving grooming also had a better than predicted change in their coat condition over the dry season, relative to their

DRS_{CV}. This cannot be explained by any direct manipulation of their own fur but could for example be mediated by the potentially stress-reducing effects of giving grooming (Shutt et al., 2007; Aureli and Yates, 2010). As described in chapter 4, grooming has been linked to lower basal and response GC concentrations in high-ranking male olive baboons (*Papio anubis*; Ray and Sapolsky, 1992). In the current study, high rates of giving grooming have been linked to lower DRS_{CV} in a potentially rank-dependent manner, as low-ranking males were observed to spend more time grooming than high-ranking males, and males that spent more time grooming had lower DRS_{CV}. Thus, the same rank-dependent difference in grooming rates may play a role in its link to resilience as well, i.e. individuals can only use grooming to mediate resilience if they groom for a substantial amount of time.

For females, the rate at which individuals received grooming was positively linked to R_{coat}, suggesting that high rates of receiving grooming could contribute to high resilience due to its beneficial social effects. Grooming represents one important mechanism for the maintenance of social bonds (Barrett et al., 1999), and strong social bonds have repeatedly been shown to be linked to fitness-relevant benefits in baboon species (chacma baboons, Silk et al., 2009). Thus, it is in line with predictions that high rates of affiliative behaviour would be connected to higher resilience, measured as better than expected average coat condition, given the females' DRS_{CV}. It is important to consider, however, that a hygienic function of grooming may contribute to, or underpin, this relationship. Previous studies have shown that grooming serves to remove ectoparasites (Zamma, 2002; Duboscq et al., 2017). So, while recent studies have mostly focused on the social aspect of grooming, there is little doubt that grooming does provide a hygienic benefit to the groomee and can thus be reasonably assumed to be linked to better coat condition. In that view, individuals that receive grooming at high rates might have a lower ectoparasite load and thus better than predicted coat condition based on their DRS_{CV}, compared to individuals who receive less grooming while having comparable demonstrated reactive scope.

Finally, some associations between behavioural rates and resilience measures in females contrasted with predictions. Firstly, R_{coat} was negatively linked to rates of scratching and all self-directed behaviours, in that females who showed higher rates of scratching and self-directed behaviours had worse than predicted average coat condition based on their DRS_{CV}. However, these links may provide evidence rather for a mechanistic link between R_{coat} and behaviours that directly manipulate the fur, such as scratching and self-grooming. For example, high rates of scratching could reflect a high ectoparasite load, where individuals that are infected with more ectoparasites experience more itching and therefore show higher rates of scratching. Subsequently, more scratching could lead to a worse coat condition than predicted for their DRS_{CV}, compared to females with similar demonstrated reactive scope but lower ectoparasite load. A positive link between scratching and lice load has for example been shown in Japanese macaques (*Macaca fuscata*; Duboscq et al., 2016). However, this finding and explanation are in direct contrast to the above described positive link between self-directed behaviour and resilience found in both males and females, where high rates of scratching and other self-directed behaviours were associated with higher resilience, measured as R_{temp}, thought to reflect behaviourally mediated resilience.

Finally, in females, the rate of aggression was also negatively linked to one measure of resilience, i.e. R_{change}. Here, females that showed aggression at high rates had worse development of their coat condition than predicted given their DRS_{CV}. In chapter 4 it was reported that high rates of aggression were linked to lower DRS_{CV} in a rank-dependent manner, as high-ranking females were significantly more aggressive than low-ranking females and had lower DRS_{CV} the more aggressive they were. However, in the current chapter, high rates of aggression are linked to lower resilience. This goes against the prediction that females might use aggression as a mediator of their resilience, and instead may reflect the differences in resilience by rank found in females: as described under prediction 1ii, high-ranking females had lower R_{change} than low-ranking females, while also showing higher rates of aggression. Thus, the association between high rates of aggression and low R_{change} is probably explainable by the rank difference found in resilience, and less linked to the aggressive behaviour itself.

In summary, the analyses presented here provide evidence that resilience might be behaviourally mediated in the study troop, as high rates of certain behaviours, i.e. scratching and other self-directed behaviours in males and females, and giving grooming in low-ranking males, were linked to high resilience.

Prediction 3ii: High resilience is linked to strong social bonds, reflecting social resilience.

It was predicted that strong social bonds would be linked to higher resilience, especially in females. This was based on the evidence that study females experienced social buffering through strong social bonds, as females with stronger strongest bonds had lower mean fGCM concentrations. However, no beneficial link between strong social bonds and resilience was found, but some weak evidence seen for a negative link between the number of strong bonds and R_{temp}. In males, the number of weak bonds had been negatively linked to mean fGCM concentrations. A similar effect was found in males' resilience: here, a high number of strong bonds was also linked to lower R_{temp}.

Strong and consistent social bonds have been shown to be an important factor regarding females' fitness, as they have been linked to enhanced infant survival in yellow baboons (*Papio cynocephalus*; Silk et al., 2003) and chacma baboons (*Papio ursinus*; Silk et al., 2009) and increased female lifespan in yellow baboons (Silk et al., 2010b; Archie et al., 2014) and blue monkeys (*Cercopithecus mitis stuhlmanni*; Thompson and Cords, 2018). Additionally, the number of weak social bonds has been linked to increased infant survival in chacma baboons, although this might reflect group-size effects (McFarland et al., 2017; Silk et al., 2018). In male macaques, strong bonds have also been connected to future cooperation (Barbary macaques [*Macaca sylvanus*; Berghänel et al., 2011]) and higher reproductive success (Assamese macaques [*Macaca assamensis*; Schülke et al., 2010]), as well as to lower fGCM concentrations in times of stress (Barbary macaques; Young et al., 2014). In line with predictions and earlier research, in chapter 4 it was found that strong social bonds were linked to lower average fGCM concentrations in females of the study troop, in accordance with the social buffering hypothesis, while in males a high number of weak bonds was linked to lower mean fGCM concentrations, indicating a beneficial effect of general connectedness. Based on these findings, it was predicted that social buffering might have a more general effect on individuals' fitness, and that resilience might provide a comprehensive framework, which could explain the link between sociability, physiological measures of stress, and fitness. However, in this chapter no evidence was found for a beneficial effect of social bonds on resilience, or vice versa. Instead, there was some weak evidence for a negative link between the number of strong bonds and R_{temp}. In males, this mirrors the findings of chapter 4: there, a high number of weak bonds was linked to lower fGCM concentrations. Due to the limited number of troop members, the number of weak and the number of strong bonds are correlated, so individuals with many weak bonds and low fGCM concentrations also have only a few strong bonds and with it higher R_{temp}. Therefore, even though fGCM concentrations were associated with the number of weak bonds, while R_{temp} linked to the number of strong bonds, these probably reflect the same trend of sociability being 'stressful' or costly in males.

In females, this result is more surprising, as having very strong social bonds was clearly linked to lower mean fGCM concentrations, as described above. Thus, there are three potential explanations for the findings of the current chapter: (i) having many strong bonds is costly, for example due to an energetic or time trade-off between being social and maintaining such relationships, and time spent feeding or on other aspects of self-maintenance. Maintaining strong social bonds is time consuming, based on the definition of a strong bond here, which is that the individuals of the dyad spend more time in close proximity, in body contact, or grooming than the average dyad does. Therefore, if an individual has many above-average strength bonds, it might need to spend more time on maintaining these relationships than an individual that only has a few strong bonds does and might therefore have less time and energy available to forage, feed, or perform other aspects of personal maintenance. Testing this idea is difficult, however, as energetic challenges would be indicated by higher GC levels, while strong social bonds have a mitigating effect on HPA-axis activation; (ii) being selective and thus only having a few strong bonds might be beneficial. A study on female chacma baboons (*Papio ursinus*), for example, found that females had lower fGCM concentrations when they focused their grooming on a smaller number of partners (Crockford et al., 2008). In this current study, females with a small number of strong bonds might have even stronger strong bonds than females who have many strong bonds but maintain these at a level just above average. To investigate this idea, one would need to test whether the number of strong bonds and the strength of the strongest bonds are correlated, but this has not been done in the context of this study. Also, the strength of the strongest bonds was not associated with any measure of resilience, as it was with mean fGCM concentrations, suggesting that it is indeed the number of bonds that links to resilience, and not their strength; (iii) finally, how the number of strong bonds links to R_{temp} in females might be better described by a non-linear relationship. The full model including the number of strong bonds had a higher AIC_C than the null model, and some assumptions of linear models were violated regarding the linearity of the relationship between predictors and the response variable. Thus, the relation between the number of strong bonds and R_{temp} could potentially be better described by a different relationship, such as a negative quadratic function. There might be a range of optimal number of strong bonds that would be connected to high resilience, while very small numbers of bonds would be linked to social isolation, missing social buffering, and low availability of social support, while very large numbers of social bonds could lead to the above described trade-off in time and energy needed to maintain these relationships and self-maintenance. This idea would be in line with a recent study of prairie voles (*Microtus ochrogaster*) that found that individuals with an intermediate number of social partners had the highest reproductive success (Sabol et al., 2019). However, while this is a very appealing model, a larger number of samples and a more precise prediction in this regard would be needed to test it here. Overall, this chapter provided no evidence that resilience might be mediated via strong social bonds in the study troop.

Prediction 3iii and 3iv: High resilience is linked to high centrality in the affiliation and in the agonism network, reflecting social resilience.

Regarding social resilience, it was also predicted that a highly central position in the affiliation network and/or in the agonism network would be linked to higher resilience. However, regarding the affiliation network, only females' R_{change} was connected to the individual clustering coefficient, in that females which were more cliquish had lower resilience than females which were less cliquish, but no measure of direct centrality in this network was linked to resilience in either males or females. Regarding the position in the agonism network, having a large network as indicated by high reach was linked to low R_{temp} in males and high R_{coat} in females. Furthermore, high betweenness centrality was connected to high R_{temp} in females, but not males.

Previous studies have shown that position in an affiliation network can be connected to fitness-relevant measures. In female chacma baboons (*Papio ursinus*), for example, high eigenvector centrality in an affiliative network was linked to higher infant survival (Cheney et al., 2016) and focused grooming networks were connected to reduced stress reactivity (Wittig et al., 2008), while in rhesus macaques (*Macaca mulatta*) a small network as reflected by low reach was associated with lower GC concentrations in high-ranking females (Brent et al., 2011). In line with these patterns, in chapter 4 it was found that high centrality in the affiliation network was linked to lower mean fGCM concentrations in females of the study troop, but to higher mean fGCM concentrations in males. While this indicated that a high degree of sociability might be beneficial for females but might be more challenging for males, there was only weak support that this effect extended to resilience. Here, only clustering coefficient was linked to resilience, with females having a high clustering coefficient and thus a high cliquishness having lower R_{change}, indicating that generally having a smaller network and being more cliquish might be connected to a poorer ability to cope with the dry season.

Regarding agonistic networks, a high degree and low clustering coefficient in an agonism network were predictive of survival during extreme weather in Barbary macaques (*Macaca sylvanus*; Lehmann et al., 2015). In line with this, analyses in chapter 4 indicated that high centrality in such a network was linked to lower demonstrated reactive scope in both males and females, and that low clustering was connected to lower mean fGCM concentrations in females. As discussed there, these findings provide a potential explanation of how social integration might be linked to higher survival probability, as high centrality and low cliquishness were connected to attenuated stress reactivity and lower mean physiological stress response levels, which in turn are likely beneficial when coping with extreme weather conditions. In females, the idea that good social integration, here measured as reach and centrality in an agonism network, might be linked to fitness benefits was supported by the associations found here, as both having a large network and being central in the agonism network were connected to higher resilience. More specifically, females that had a larger network, as reflected by high reach, had higher R_{coat}, which was thought to reflect the long-term resilience of the individual cumulating in the better than expected average coat condition, given their DRS_{CV}. Additionally, females with high betweenness centrality, i.e. females connecting otherwise unconnected individuals, had higher R_{temp}, which reflects a better coat condition than predicted given their DRS_{CV} at the end of the study period. For males, however, the findings contrast with the predictions, with previously published work, as well as with the findings of chapter 4: there, high eigenvector centrality in the agonism network was linked to lower demonstrated reactive scope, while here, high reach reflecting a large network was connected to lower resilience, measured as R_{temp}. While this could suggest a difference between the effects of network position on physiological stress response measures and measures of resilience, it is more likely that single data points have a strong impact here. Visual inspection of the data (Figure 5.33) shows that all but two males have very similar scores of reach, i.e. a reach between 0.73 and 0.79. The other two males have reach scores between 0.50 and 0.59 and high R_{temp} values. In comparison to females, there is thus very low variation in reach of males, which potentially leads to a strong effect of the lower two reach data points on the relation of reach and R_{temp}, so this link should be interpreted cautiously.

Overall, this chapter found only weak evidence for a negative link between the degree of clustering in an affiliative network and resilience in females, but stronger evidence for a positive link between centrality and network size in an agonistic network and females' resilience. There was, however, no support for a connection between affiliative network position and resilience in males, and only a doubtful link between centrality in the agonism network and resilience.

5.5.3 Conclusions and future directions

This chapter explored the usefulness of IRT in quantifying coat condition of wild animals and developed *delta coat temperature* as a new measurement for this purpose. Further studies would benefit from investigating the link between coat condition, e.g. measured as delta coat temperature, and physiological measures of well-being to validate coat condition as a proxy of general condition. Based on the results presented in this chapter, IRT appears as a promising tool to assess coat condition in wild animals, quantitatively and non-invasively.

Additionally, this chapter explored the use of the concept of resilience in the study of inter-individual differences in coping abilities in wild animals. While resilience as a term has often been used, this study is the first to my knowledge to conduct an exploration based on a testable framework such as the ‘three-hit concept’ (Daskalakis et al., 2013). Based on a precise definition of resilience as “a relatively good outcome despite risk experiences” (Rutter, 2012), new measures of resilience were developed to assess resilience in wild animals quantitatively and non-invasively, by quantifying whether individuals fared ‘better’ or ‘worse’ than predicted by their demonstrated reactive scope and relative to their conspecifics. As resilience describes a process and can only be observed after risk experiences, the question of how to validate these measures is not trivial and will need further exploration. Nevertheless, this chapter provided a first step by linking the proposed measures of resilience to biologically relevant factors such as age, rank, and reproductive success. A further area of enquiry would now be to investigate whether these measures of resilience are linked to genetic predispositions, early-life experiences as well as to measures of fitness and long-term health. This chapter provided evidence that displacement behaviours not only function as coping behaviours but might also mediate resilience more generally. Furthermore, it provided further support for the idea that agonistic social networks are a useful tool to investigate individuals’ general level of social integration, and that this integration might be beneficial regarding resilience. Consequently, the findings of this chapter encourage further investigations into displacement behaviours as well as agonistic relations, two relatively understudied groups of behaviours, in the context of coping, resilience, and fitness.

6. General discussion

The aim of this thesis was to explore the process of resilience in a comprehensive manner, by describing physiological measures as proxies of stress and stress reactivity in a mountain population of chacma baboons, investigating these animals' physiological and behavioural responses to adverse situations, and exploring the concept of resilience using fitness-relevant measures. In this chapter, I will first give a summary of the key findings this study produced, and then discuss the broader topics that emerged, specifically: regarding the questions what insights can be gained by analysing both mean physiological stress response levels and stress reactivity in wild animal populations; whether the same types of behaviour are linked to the process of coping and to resilience; whether the effects of social bonds and social integration are comparable; and finally, whether resilience is a useful and practical framework to use in the study of wild animals.

6.1 Summary of key findings

This thesis followed a three part approach in investigating resilience, in this way reflecting the stages of the process of resilience: chapter 3 described levels of a physiological mediator (fGCM concentrations) connected to responses to environmental stimuli as well as metabolic processes, and investigated the effect of predation events and weather on this mediator; subsequently, chapter 4 explored the use of coping behaviours in the study animals, describing behavioural responses to predation and baiting as exemplary adverse situations, and investigating links between short-term changes in behaviour and long-term behavioural rates, and physiological stress response measures; finally, chapter 5 explored the use of the concept of resilience in the study of wild animals and developed measures of resilience that can be used non-invasively, as such investigating the cumulative effects of coping processes on longer term success in a fitness-relevant context.

In chapter 3, I investigated whether different demographic and environmental factors are linked to physiological stress response measures and compared the links between these factors and (i) mean physiological stress response levels and (ii) demonstrated reactive scope, used as a proxy of stress reactivity. This provided a first description of stress physiology measures in this population, one of the first investigations of demonstrated reactive scope, and formed the basis for the subsequent analyses into coping and resilience in this population. Regarding demographic factors, females had higher demonstrated reactive scope than males, while mean fGCM concentrations did not differ between the sexes. Based on these findings, all subsequent analyses were conducted separately for the two sexes. Regarding the change of physiological stress response measures with age, adolescent and old males had lower mean fGCM concentrations than young males, and similarly, old females had lower concentrations than middle-aged females, suggesting that mean physiological stress response levels might show an inverse U-curve development over the adolescent and adult time periods. While old males had higher demonstrated reactive scope than middle-aged males, no age-related change in this proxy of stress reactivity was found in females. For females, lactating females had lower mean fGCM concentrations than cycling or pregnant females, and there was some evidence that they might experience environmental constraints differently, as only in lactating females it was found that fGCM concentrations were negatively related to minimum daily temperature. Similarly, minimum temperature was negatively correlated with fGCM concentrations in males, and maximum temperature negatively associated with fGCM concentrations when all females were considered, indicating that the baboons of the study troop might generally face challenges due to low temperatures instead of experiencing heat stress. Furthermore, high rank was strongly linked to high mean fGCM concentrations in females, but not males. Finally, the death of an adult female due to predation was associated with an increase in fGCM concentrations in the subsequent month in females, while there was no associated increase in males.

Based on these findings, coping as the behavioural response to assumed adverse events was explored in chapter 4, and the link between these behavioural responses and physiological stress response measures investigated. Additionally, I assessed whether long-term rates of behaviour were associated with physiological stress response measures, reflecting coping, and whether there was any indication of social buffering, with strong bonds or centrality in social networks being connected to lower physiological stress response measures. Both males and females responded with increased rates of self-directed behaviour to baiting (an artificially created situation of potentially high arousal or stress), and females responded in a similar fashion to predation events. In females, these behavioural responses were associated with higher demonstrated reactive scope in the case of predation and with higher mean fGCM concentrations in the case of baiting. Regarding longer-term coping, different behaviours were linked to demonstrated reactive scope in a sex- and rank-specific manner: in males, low-ranking individuals showed higher rates of giving grooming, and here high rates were linked to lower stress reactivity; in females, high-ranking individuals were more aggressive than low-ranking individuals, and females that were more aggressive had lower demonstrated reactive scope. Finally, this chapter provided evidence for social buffering both via strong social bonds and social integration in agonistic and affiliative networks in females, while in males only one measure of social integration – centrality in an agonistic network – was linked to lower demonstrated reactive scope, highlighting the importance of investigating social integration via agonistic networks in addition to affiliative social networks.

Finally, in chapter 5 I explored the use of IRT in quantifying coat condition and developed measurements of resilience, based on three scores of coat quality as well as demonstrated reactive scope. These three measures reflect different aspects of resilience, i.e. either the long-term effects of resilience, the short-term resilience to the challenges of the current dry season, or resilience measured at the end of the dry season based on a quantitative coat condition measurement. Results of the subsequent analyses varied for the different measures of resilience, reinforcing the idea of the three measures reflecting different aspects of resilience. Based on these different measurements, there was evidence that old females had lower resilience than young adult females, that high-ranking females had higher values for one measure of resilience (reflecting resilience in the longer term) than low-ranking females, but lower resilience based on a measure thought to reflect the ability to cope with the challenges of the current dry season, and that higher mean fGCM concentrations were connected to lower resilience in females. Females that had a high number of surviving offspring in the last three years had higher scores for one measure of resilience (thought to reflect longer term resilience), but lower values for a measure assumed to reflect resilience to the challenges connected to the current dry season, and females that had lost at least one infant in the last three years had lower resilience than females that did not. Regarding behavioural or social resilience, there was evidence that high resilience was linked to high rates of giving grooming in males, while in both sexes rates of scratching and other self-directed behaviours were positively linked to resilience, both results indicating behaviourally mediated resilience. Surprisingly, there was no evidence that high resilience was mediated by strong social bonds, but contrastingly there was some evidence to suggest that a high number of above average social bonds was linked to lower resilience. However, high centrality in the agonistic social network was associated with higher resilience in females, while centrality here was connected to lower resilience in males. These results indicate that resilience is not socially mediated in males, and that in females only general integration into the troop is connected to higher resilience.

6.2 What insights can be gained by analysing both mean physiological stress response levels and stress reactivity in wild animal populations?

The general stress response describes a complex physiological and behavioural process in response to an adverse stimulus, that includes many neural and neuroendocrine responses. While the HPA-axis only represents one part of this process, GC concentrations have long been used as measurements of the stress response due to the practicability and possibility to collect samples non-invasively. fGCM concentrations have been shown to increase after the experience of a stressor in many mammal species (Romero and Wingfield, 2015). Nevertheless, the use of GCs, and specifically the use of the term ‘stress hormone’, has recently received increased critical attention as GCs are generally reflective of metabolic processes (Haase et al., 2016; MacDougall-Shackleton et al., 2019). Therefore, a stressor was defined in the context of this study as an actual or perceived threat to any aspect of homeostasis, that would lead to an increase in GC concentrations reflective of the increased energetic demands that are linked to coping with the adversity (MacDougall-Shackleton et al., 2019). While a stress response of appropriate strength for the adversity experienced or expected is necessary for successful coping, even these appropriate responses can have negative consequences if they occur at high frequency (Taff et al., 2018), and hyperreactivity of the stress response or prolonged high stress response levels, e.g. due to inefficient negative feedback, can be linked to fitness-relevant negative outcomes, such as reduced wound healing (DuRant et al., 2016). Therefore, lower fGCM concentrations (and to a certain degree also lower stress reactivity) have been assumed to be beneficial in the long term in the context of this study.

While many studies use either mean fGCM levels or raw or monthly fGCM concentrations depending on the practicalities of sample collection, there are certain other aspects of the physiological stress response that also have been studied extensively. As one of these, stress reactivity has received particular interest. Reactivity has been defined as "the deviation of a physiological response parameter(s) from a comparison or control value that results from an individual's response to a discrete, environmental stimulus" (Matthews, 1986) and as such describes the strength of the neuroendocrine response to an adverse situation in the context of stress. As described in chapter 1, it is difficult to ascertain the degree of stress reactivity in wild animals, so that based on the reactive scope model (Romero et al., 2009), the demonstrated reactive scope has been proposed to quantify non-invasively the range of mediator an individual uses to cope with life's challenges (MacLarnon et al., 2015). As such, repeated high stress reactivity is assumed to be reflected by a large range of mediator used, while low stress reactivity would be reflected by a smaller range of mediator observed in the longer term. Until now, only a few studies have investigated reactive scope or demonstrated reactive scope in wild animals (e.g. Romero, 2012; MacLarnon et al., 2015; DuRant et al., 2016; Zhang et al., 2018; Tkaczynski et al., 2019; Young et al., 2019), so this study provides a first comparison between mean physiological stress response levels and stress reactivity, and how they link to demographic and social factors.

When considering the results of both chapter 3 and 4, a relatively clear picture emerges regarding what kind of factors link to either mean physiological stress response levels or to stress reactivity. Demographic factors, to the extent that they could be investigated in this study, are linked almost exclusively to mean physiological stress response levels, in that mean fGCM concentrations increased in middle-aged individuals and then decreased again in older age in both males and females, and that high-ranking females had higher mean fGCM concentrations than low-ranking females. As there was only evidence in males that demonstrated reactive scope might increase in old individuals and sample sizes of old males were low, the physiological changes linked to ageing and to dominance rank acquisition seem to primarily affect measurements of mean physiological stress response levels, and less so the reactivity or range of mediator an individual utilises.

While the link between long-term physiological stress response measures and short-term changes in behaviour was complex and dependent on both sex and situation, the picture regarding long-term use of coping behaviours and sociability was clearer. Social buffering, via strong social bonds and integration into an affiliative network, was exclusively linked to mean physiological stress response levels in females, while the use of coping behaviours and integration into an agonistic network were associated with stress reactivity in both sexes. The effect of social buffering has previously been observed in chimpanzees (*Pan troglodytes*) as the reduction of uGCM concentrations not only in stressful agonistic situations, but also in affiliative or neutral situations, showing that being in the proximity of a bonded partner was associated both with reduced uGCM levels during affiliative and neutral situations as well as with reduced stress reactivity during inter-group encounters (Wittig et al., 2016). Accordingly, in this current study, strong social bonds were linked to lower mean physiological stress response levels in female baboons, but not to reduced stress reactivity, which is in line with the idea of social bonds having a ‘stress buffering’ effect across contexts. Contrastingly, lower demonstrated reactive scope was associated with high rates of giving grooming in (low-ranking) males and high rates of aggression in (high-ranking) females, as well as with social integration in the agonism network in both sexes. These results fit with the assumption that demonstrated reactive scope reflects stress reactivity, as coping behaviours such as grooming or aggression are thought to attenuate the physiological stress response (Wechsler, 1995) and thus lead to a lower observed range of mediator used over time. Similarly, good social integration might render a high stress reactivity unnecessary, and it makes sense therefore that such integration was associated with lower demonstrated reactive scope, but different interpretations of this link will be discussed below.

Overall, these results indicate that mean fGCM concentrations and demonstrated reactive scope do indeed reflect different aspects of the physiological stress response system. While it would be beneficial to explore more ways of measuring stress reactivity directly in wild animals in the future, demonstrated reactive scope was shown here to be linked to both coping behaviours and social integration and appears to present a suitable, if potentially crude, non-invasive measure of stress reactivity. Thus, future studies will benefit from considering both the absolute physiological stress response levels and a measure of stress reactivity, as these were found in this study to be differently linked to demography, behaviour, and sociability.

6.3 Are behaviours linked to the process of coping and to the measures of resilience in a similar way?

Coping behaviour, as described in the introduction, has been defined as a behavioural reaction to an aversive situation (Wechsler, 1995). In non-human primates, socio-positive behaviours, such as grooming, aggression, and self-directed behaviours have been proposed as potential coping behaviours (Gustison et al., 2012). Indeed, both males and females of the study troop showed increases in scratching and other self-directed behaviours as apparent coping behaviour in response to baiting, and females showed elevated scratching in response to predation.

In the longer term, it was thought that differential use of coping behaviours would lead to variation among individuals in long-term behavioural rates, and that how these link to physiological stress response measures would reflect long-term mitigation of stress responses. In line with this, lower stress reactivity (as shown by lower DRS_{CV}) was associated with high rates of giving grooming in males and high rates of aggression in females, potentially in a rank-related manner. In the context of this study, I suggested that potential coping behaviours might also link to the measures of resilience developed in chapter 5. Coping behaviours represent the behavioural part of the individual's response to a stressor and as such make up one step in the process of resilience, i.e. high resilience needs successful use of coping behaviour. Thus, it is valuable to explore the three potential coping behaviours in relation to their links to physiological stress response measures and to resilience.

As described above, scratching and other self-directed behaviours increased during baiting in both sexes, and in females also after predation events. In chapter 4, I argue that one of the most effective coping behaviours in the context of predation is likely to be aggressive behaviour towards the predator, such as mobbing, and that males might be more suited to show mobbing behaviour, which would explain why they did not appear to use scratching to cope with predation events. Rates of scratching were, however, not linked to either short-term changes in fGCM concentrations during these events or to long-term mean physiological stress response levels or demonstrated reactive scope. Nevertheless, there was strong evidence that these displacement behaviours mediate resilience, as both males and females with high rates of scratching and other self-directed behaviours had higher resilience (measured as R_{temp}). These results indicate that displacement behaviours have a beneficial effect in their role as coping behaviours, even though they might not mitigate the physiological stress response. This in in accordance with a study in rats (*Rattus norvegicus domestica*), where individuals that used displacement behaviours during tail-shock experiments showed no increase in anxiety-related behaviours afterwards, but did still show the same physiological responses to the stressor as control animals did (Helmreich et al., 2012).

The fact that self-directed behaviours were increasingly shown during or after aversive situations supports the use of displacement behaviours as an indication of arousal or anxiety (as used by e.g. Schino et al., 1988; Castles et al., 1999; Semple et al., 2013). However, in accordance with previous studies (Higham et al., 2009; Gustison et al., 2012), there was no link between rates of displacement behaviour and mean physiological stress response levels or stress reactivity, indicating that these behaviours should not be used as measures of ‘stress’ in place of physiological stress response measures. Overall, this study provided evidence that chacma baboons use displacement behaviours to cope with stressful events, and that the increase in response to strong stimuli such as baiting or predation can be observed over the following two days. In combination with their link to high resilience, displacement behaviours may play a more important role than often assumed and should be included in investigations regarding the link between sociability, fitness, and resilience.

Regarding socio-positive behaviour, there was no evidence that individuals of either sex increased their rates of grooming directly after an aversive situation, but in males, high long-term rates of giving grooming were associated with lower stress reactivity. Fittingly, males' high rates of giving grooming were also linked to higher levels of one measure of resilience, which reflected a better development of coat condition over the dry season than was predicted given their DRS_{CV}. Evidence indicated, however, that grooming was a coping behaviour mostly shown by low-ranking and less by high-ranking males, potentially reflecting rank-dependent opportunities to express affiliative behaviours. Either way, grooming in male baboons has received very little attention, besides a study of Ray and Sapolsky (1992) showing that in high-ranking male olive baboons (*Papio anubis*), high rates of affiliation both within and outside of the consortship context were linked to lower baseline and response GC concentrations, and a study in kinda baboons (*Papio kindae*) showing that males often initiated grooming bouts with females (Weyher et al., 2014). The results presented in the current study reinforce the value of studying socio-positive behaviours in males, as these behaviours linked to both stress reactivity and resilience and therefore might play an important role in mediating males' fitness.

In female baboons, grooming has been studied more in-depth, for example regarding the link between the size of a female's grooming network and fGCM concentrations (e.g. Crockford et al., 2008) or in its role as a tradeable commodity (Barrett et al., 1999). While I did find evidence that strong social bonds have a beneficial effect regarding their mean physiological stress response levels in females, as will be discussed further below, and social bonds are maintained by affiliative behaviour, rates of giving grooming specifically were not linked to any measure of physiological stress response or resilience in this troop's females. This contrasts with a vast literature that has focused on the 'tend-and-befriend' hypothesis, especially in humans. This hypothesis suggests that while males show 'fight-or-flight' responses to threat, females would do so less often and rather show tending behaviour towards infants in the short-term, and befriend other females to build a network of support in the long-term (Taylor et al., 2000). In line with this proposition, a large proportion of studies on non-human primates have focused on the benefits of socio-positive behaviour in females. And while studies do indicate that female chacma baboons (*Papio ursinus*) utilise affiliation to cope with the loss of relatives in the longer term (Engh et al., 2006a), an investigation into Barbary macaque (*Macaca sylvanus*) females' short-term responses to mildly stressful events did not find an increase in affiliation (Gustison et al., 2012). As females of the study troop also showed no change in grooming behaviour in response to stressful situations and neither were long-term rates of grooming linked to mean physiological stress response levels, stress reactivity, or resilience, I would posit that, at least in this study troop, 'tending' does not represent a main response to threat.

Instead, results indicate that females, but not males, used aggressive behaviour to mediate their stress reactivity. While postulating the 'tend-and-befriend' hypothesis, Taylor et al. (2000) also described that the fight-or-flight response to stressors has mainly been studied in male animals. However, more recently studies in humans have found that exogenous GC administration leads to aggressive behaviour in response to strong provocation in women, but not in men (Böhnke et al., 2010). Similarly, in Barbary macaques (*Macaca sylvanus*), females were observed to increase their aggressive behaviour after a mildly stressful stimulus (Gustison et al., 2012) and in a separate study it was found that females used reactive aggression, in contrast to proactive aggression, in about 76% of female aggressive incidents (Paschek et al., 2019). Reactive aggression should by definition be regarded as a coping behaviour, as it is shown in response to a perceived or real threat. While in the current study no significant increase in females' aggression rates were observed in response to either baiting or predation, rates of all agonistic behaviours increased significantly during baiting, and lower demonstrated reactive scope was linked to higher long-term rates of aggression in high-ranking females. Surprisingly, there was a negative association between aggression rates and one measure of resilience in females, i.e. females that showed high rates of aggression had lower resilience, in that they had a worse than based on their DRS_{CV} predicted development of coat condition over the dry season. This, however, is likely linked to the generally lower scores in this resilience measure of high-ranking females and less connected to the rates of aggression they show, as discussed in chapter 5. So, while the results suggest that females' stress reactivity might be mediated by their aggressive stress responses, there was no evidence for such a link in males, and no positive association between aggression and resilience in either sex. Overall, similar to the findings regarding socio-positive behaviour in males, these results suggest that aggression as a stress response in female non-human primates is understudied, and that female aggression should be included in future research regarding the link between behaviour and any fitness-relevant measures.

In summary, this study showed the important role displacement behaviours play in the context of stress and resilience. Scratching and other self-directed behaviours were shown in response to adverse situations and high rates of displacement behaviours were also strongly linked to higher resilience in males and females. Regarding socio-positive behaviour, there was some evidence that males (especially low-ranking males) utilise grooming to mitigate their stress reactivity and that these males also have higher resilience to the challenges connected to the dry season. With respect to aggression, in (high-ranking) females, high rates of aggression were connected to lower stress reactivity, but they were not beneficially linked to any measure of resilience.

6.4 Are the effects of social bonds and social integration comparable?

Strong social bonds and social integration have been linked to fitness-related benefits in many non-human primate species, for example in yellow baboons (*Papio cynocephalus*; Silk et al., 2003), chacma baboons (*Papio ursinus*; Cheney et al., 2016), Barbary macaques (*Macaca sylvanus*; Berghänel et al., 2011), Assamese macaques (*Macaca assamensis*; Schülke et al., 2010), rhesus macaques (*Macaca mulatta*; Ellis et al., 2019), and blue monkeys (*Cercopithecus mitis stuhlmanni*; Thompson and Cords, 2018). The current study provides a rare investigation into the link between social bonds and social network position on the one hand and physiological stress response measures and resilience on the other, in this way illuminating one potential way in which sociability might be linked to fitness. As certain aspects of their social behaviour as well as the way in which sociability links to physiological stress response measures and resilience might differ between males and females, the sexes are discussed separately.

Females

Regarding female baboons, this study provided evidence for social bonds having a buffering effect on the physiological stress response system. In accordance with findings in chimpanzees (*Pan troglodytes schweinfurthii*; Wittig et al., 2016) and chacma baboons in the Okavango Delta (*Papio ursinus*; Seyfarth et al., 2012), both having very strong social bonds and being in a central position in the affiliation network were associated with lower mean fGCM concentrations. These results indicate an important link between social bonds and fitness-relevant physiological stress response measures, providing a potential explanation for the fitness-benefits of social bonds described in the introduction. Even though the methodology used here does not allow causal inferences, it does allow a comparison between models of different predictions, which shows that the model including the strongest strong bonds had a substantially better fit than the models including strength or betweenness centrality in the affiliation networks, indicating that the strength of the strongest social bonds explains more variation in mean fGCM concentrations than does centrality in the affiliation network. Based on this strong link between social bond strength and mean physiological stress response levels, it is surprising that bond strength was not associated with resilience in females. Instead, model comparisons suggested that having many strong bonds might be linked to lower resilience. This could be due to an energetic trade-off, where the maintenance of very strong bonds might take time that would otherwise be used for feeding or other self-maintenance, but this possibility was not further assessed here.

Instead of dyadic bonds, general social integration might play an important role in mediating resilience. High centrality and high connectedness in the agonism network were linked to both lower demonstrated reactive scope (DRS and DRS_{CV}) and higher resilience. These findings support the importance of social integration on the one hand, and of using agonistic networks in assessing social integration on the other. Strong social integration, assessed using a social network approach, has only been linked to fitness-related benefits in non-human primate species in a few studies. In female chacma baboons (*Papio ursinus*), for example, high eigenvector centrality in an affiliative network was associated with higher infant survival (Cheney et al., 2016), and in Barbary macaques (*Macaca sylvanus*), high degree in an agonistic network was linked to higher survival probability in extreme weather conditions and was a better predictor of survival than position in an affiliation network (Lehmann et al., 2015). As explored by Lehmann and Ross (2011), networks using different social behaviours, such as socio-positive, aggressive, and mating behaviours, can differ quite substantially from each other, so that networks based on different types of behaviours should be constructed to capture more of the social complexity that baboons exhibit. Besides the study in Barbary macaques (Lehmann et al., 2015), agonistic relationships have been linked to fitness benefits in marmots (*Marmota flaviventris*; Lea et al., 2010), and dominance, as expressed in an agonistic network, has been suggested to regulate affiliative relationships and stabilise network structures, thus playing an important role in constructing an individual's social niche (Barrett et al., 2012). In accordance with these studies, only high centrality assessed via an agonistic network was connected to lower stress reactivity and higher resilience here. These findings emphasise the importance of assessing social integration via agonism in addition to affiliation.

Males

For males, there was no evidence that having strong social bonds or being in the centre of an affiliative social network was linked to any beneficial effects on their physiological stress response or resilience. Instead, having many weak bonds and a low centrality in the affiliation network were linked to lower mean fGCM concentrations, and having few strong bonds was associated with higher resilience, suggesting that centrality or too many strong social bonds might be stressful or challenging rather than stress-buffering for males. This might be linked to the specific nature of strong social bonds males maintained, which were to a large part bonds to females whose offspring they likely sired, which in turn might be linked to challenges connected to defending the female and her offspring (Huchard et al., 2010), leading to the bonds being energy consuming rather than stress-buffering. Nevertheless, as for females, high centrality in the agonism network was linked to lower demonstrated reactive scope but having a large agonistic network as represented by high reach was again linked to lower resilience, the latter contrasting with the finding in females. All this suggests that being well integrated renders high stress reactivity unnecessary for males, potentially due to more stable and predictable relationships with other troop members (De Waal, 1992; Brent et al., 2011), but that this centrality is not inherently linked to lower energetic demands, stress buffering, or higher resilience. Resilience in particular might be mediated quite differently in males and females, as the sexes face very different challenges over their life.

Opposite-sex bonds

Comparing the findings of males and females also reveals that dyadic opposite-sex bonds might have different meanings or consequences for the two individuals involved. When checking the identities of the top three partners of females, it turned out that over half the females had at least one male as one of their top three partners, and three females even had two males as top partners, as described in section 2.2.2.2.

Importantly, not all of these females were lactating during the study period and it is unlikely that these bonds were solely driven by consortships either, as consortships generally only last a few days maximum. For males, almost all top three partners were females. This highlights two issues: firstly, for females having strong bonds with males and females was linked to lower mean fGCM concentrations, whereas this was not true for males. Thus, bonds that might be stress-buffering for the female might not have such a buffering effect for the male. Male chacma baboons have been shown to actively form bonds with females whose infants they likely sired (Moscovice et al., 2010; Webb et al., 2019), providing benefits for their offspring this way (Huchard et al., 2013). They have also been found to mediate a trade-off between time and energy spent protecting their infants and pursuing mating opportunities, as they tend to have elevated fGCM levels and spend more time with their bonded female and infant during times of hierarchy instability caused by immigration (Cheney et al., 2015). In combination with the findings described in the current study, this suggests that heterosexual bonds might reflect paternal- and mating-efforts in males, and that these bonds are time and energy consuming, potentially explaining why bonds were not found to be stress-buffering for males as they were for females.

Secondly, most studies investigating the link between sociability and fitness in primates have focused solely on females (e.g. yellow baboons [*Papio cynocephalus*; Silk et al., 2003]; chacma baboons [*Papio ursinus*; Cheney et al., 2016; McFarland et al., 2017]; blue monkeys [*Cercopithecus mitis stuhlmanni*; Thompson and Cords, 2018]). Other studies have shown, though, that opposite-sex bonds can be stable over long time periods (chacma baboons, Baniel et al., 2016; olive baboons [*Papio anubis*; Städele et al., 2019]; Assamese macaques [*Macaca assamensis*; Ostner et al., 2013; Haunhorst et al., 2016]), that these bonds with males can have important benefits for the female, such as reduced aggression and competition from the male (Assamese macaques, Haunhorst et al., 2017) and lower fGCM levels in certain seasons (Assamese macaques, Fürtbauer et al., 2014), and that social bonds with both males and females can predict females' survival (yellow baboons, Archie et al., 2014). While it would have been therefore interesting to compare the effect of same- and opposite-sex bond strength on females' physiological stress response levels, this was not possible here due to the way analyses were conducted. Independent of whether these bonds represent parenting- or mating-efforts on the side of the males (Städele et al., 2019), though, the results of the current study indicate that these opposite-sex bonds might play an important role in buffering females' physiological stress response system and thus both same- and opposite-sex bonds should be considered when investigating the link between females' sociability and fitness.

Overall, this study highlights the value of studying the impact of both social integration and social bonds in primates. It shows that having strong social bonds might be linked to different aspects of the animals' stress physiology and resilience than those to which being well-integrated might be linked and emphasises the importance of assessing integration both via affiliative and agonistic social network position, especially but not solely when investigating male sociability. However, a correlational study like this cannot as such clarify whether social integration is beneficial due to the availability of social support, the predictability of interactions, or other fitness-benefits linked to high centrality, or whether individuals that have lower stress reactivity (and higher resilience) inherently are better able to maintain central positions in the troop.

6.5 Is resilience a useful and practical framework in the study of wild animals?

Resilience, even though it was originally a psychological concept, is a frequently used term in animal research but one that is often ill-defined, as described in chapter 1. Thus, this study had the goal of selecting a working definition of resilience which can be used in the study of animals' inter-individual variation in fitness, i.e. "a relatively good outcome despite risk experiences" (Rutter, 2012), and then developing measurements of resilience that can be used non-invasively. In this context, it is important to recognise that this study is limited by the amount and particularly duration of data collected; ideally, measures of resilience would rely on data on longevity and reproductive success but such longitudinal data, which would be collected during multi-generational studies, are not available in a study such as this one.

Nevertheless, I would argue that the measurements developed in this study are both useful and meaningful. As described in chapter 5, R_{coat} was assumed to represent the long-term resilience that culminates in the current coat condition in relation to the reactive scope needed to maintain it; R_{change} was thought to reflect the individual's resilience to the challenges connected to the dry season during which the change in coat condition and the demonstrated reactive scope were assessed; and R_{temp} was proposed to reflect the, quantitatively assessed, coat condition at the end of the study period and thus at the end of the dry season relative to the demonstrated reactive scope. While a validation of these measures based on lifetime fitness was not possible (as described above), each measure did link to a specific demographic or physiological factor in females in agreement with some of the predictions: R_{coat} was lower in older than in younger females, potentially reflecting the decline in resilience and general condition in older age, was higher in high-ranking than in low-ranking females, potentially linked to potential benefits of high rank, and was higher in females with more surviving infants, reflecting their higher long-term resilience and associated ability to successfully reproduce. R_{change} was lower in high-ranking compared to low-ranking females, potentially revealing that high-ranking females might need to exert more energy than low-ranking females to cope with the challenges of the dry season, which fits the finding that high-ranking females had higher mean fGCM concentrations as well. Additionally, R_{change} was lower in females with more surviving offspring in the last three years, indicating that while their long-term resilience, as reflected by R_{coat}, might be higher and enable them to reproduce more successfully, raising offspring might still come with a cost to resilience and condition in the shorter term, as indicated by their worse than based on their DRS_{CV} predicted change in coat condition over the dry season. R_{temp}, finally, was negatively associated with mean fGCM concentrations, suggesting that females with higher mean physiological stress response levels had lower resilience. As just stated, high mean fGCM concentrations reflect the apparent need to mobilise energy to cope with challenges, which in turn can lead to worse coat condition at the end of the dry season relative to their demonstrated reactive scope. These differential associations between the different resilience measures and demographic and physiological factors lend support to the meaningfulness of the proposed measurements, even though further studies with longer-term data will be needed to validate them as measures of resilience, as described above.

Interestingly, and in contrast to what was seen in females, resilience measures in males were not connected to any demographic or physiological characteristics. This might be explained by sex-specific trade-offs between reproduction and self-maintenance, where males might invest more in the current reproductive success and with it faster development and bolder behaviour, whereas females might invest more in self-maintenance and future reproductive opportunities, which could explain differences in mortality, senescence, and lifespan (Hämäläinen et al., 2018). Based on data from yellow baboons (*Papio cynocephalus*) at Amboseli in Kenya, for example, males experience higher initial mortality at the onset of adulthood and a stronger increase in mortality with older age than females (Bronikowski et al., 2011; Alberts et al., 2014). Yellow baboon males and females were, however, found to similarly decline in their body condition, have higher gastro-intestinal parasite load, and experience more incidences of illness with older age, while males additionally rapidly decline in social status with old age (Alberts et al., 2014), all of which suggests that old age should be linked to lower resilience in males of the study troop. However, in contrast to females, this was not the case here, and there are at least two possible explanations for this: firstly, yellow baboon males have a life expectancy several years shorter than females (Bronikowski et al., 2011); assuming that life expectancies are similar in chacma baboons, this could lead to females of the study troop reaching a greater age and thus experiencing a stronger decline in resilience, while males might not reach an age where resilience would have measurably declined. Secondly, it is also possible that due to the higher mortality of males compared to females, relatively fewer old males were present in the study troop. Based on the age classes described in this study, only two males were categorised as ‘old’, making statistical conclusions about age effects in males generally difficult.

Another finding in the yellow baboons (*Papio cynocephalus*) was that old males declined rapidly in social status, and that low rank was connected with higher fGCM levels and slower wound healing in males (reviewed in Alberts et al., 2014). These findings suggest that low rank should be connected to lower resilience in males, but no such connection was observed in the study troop. Generally, the study troop described here seemed to differ from the ‘typical’ baboon troop regarding rank-related costs and benefits: across social species it has been observed that animals fight for dominance and that high rank is associated with fitness-relevant benefits, such as preferential access to food and mating opportunities and generally greater reproductive success (reviewed in Majolo et al., 2012). In the study troop, however, high rank in females was linked to higher mean fGCM concentrations and lower resilience, while there were no apparent differences by rank for males. Additionally, while no long-term data on reproductive success was available, males of all rank categories had consortships and were likely to have sired offspring during the last three years, based on observations of matings and male-female bonds after parturition, and females of all rank categories produced offspring. While I did not collect data on access to food patches, most food items in the troop’s home range were widely spread and mostly not monopolisable. Also, while high-ranking females were more aggressive than low-ranking females, females of low rank did not receive more aggression than females of high rank. In circumstances like these, it is questionable what kind of costs are connected to low rank, and I would suggest that, in accordance with the idea that habitat characteristics shape sociality (Hinde, 1983), baboons in a montane habitat might differ substantially from baboon populations in savannas or deserts in relation to the costs and benefits associated with dominance rank. If only low or no costs are connected to low rank, then that might explain why there were no rank-related differences found in either mean physiological stress response levels, stress reactivity, or resilience in males; an absence of (significant) costs of low rank in females may also help to explain why lower rank was actually connected to lower mean fGCM concentrations and higher values of one measure of resilience compared to high rank.

Either way, resilience does appear to be a useful and practical concept to investigate inter-individual differences in physiology, sociability, and fitness. The measurements proposed here can easily be transferred to other species and adapted for the specific practicalities of field work. Additionally, they can be used non-invasively, but could be refined using other invasive or non-invasive physiological or genetic measures, as well as longer-term data on reproductive success, body or coat condition, and longevity. When long-term data are available, it would be even possible to incorporate early-life experiences or genetic data to assess their effect on later-in-life resilience. Considering these points, the framework of resilience can then be used to investigate further research questions in the field of inter-individual differences in fitness, as will be described below. Thus, I conclude that the framework of resilience based on the three-hit-concept, and on the definition of relative success, is useful and would recommend other studies to incorporate it, which would then allow a comparison of the different factors that might affect resilience across habitats or species.

6.6 Limitations, conclusion, and outlook

This study had to contend with some limitations, including practical problems like permit issues, limited time available to collect data, and difficult fieldwork conditions leading to potentially uneven data collection, especially of faecal samples, regarding individuals and time of day, and comparatively short and low observation times. It also needs to be considered that most observations and results described in this study are of a correlational nature, which means causal inferences can only be speculative. In addition, the nature of this study was to a large part exploratory, as it aimed to provide a new approach to studying resilience in wild animals, and therefore a large number of statistical analyses were conducted increasing the probability of false positive results (but an Information Theoretic Approach was utilised in a large part of analyses to reduce this probability). Furthermore, no data on kinship and matrilines were available, both of which might affect findings linked to the individuals' physiology and sociability, and it was not possible to collect data on the whole group due to the large troop size, thus potentially important interaction partners might have been excluded from analyses. Lastly, categorical classifications of age and dominance rank position were used throughout with low numbers of individuals in certain categories, which complicates interpretation of results occasionally.

While future use of the developed measures is certainly needed to assess their value and validity, this study provided a comprehensive investigation into the different steps involved in the process of resilience. It described fGCM concentrations as a measure of physiological stress response levels in response to predation, climatic variation, and baiting, and used demonstrated reactive scope as a proxy for stress reactivity. In this way, it provided new insights regarding the link between environment and stress physiology as well as regarding differences in stress physiology based on demographic classifications. It subsequently explored the use of coping behaviours in response to predation events as a naturally occurring stressor, and baiting as an artificial stressor, and investigated how coping behaviours and sociability linked to physiological measures in the longer term. Finally, it explored the use of the concept of resilience in the study of wild non-human primates, the validity of the newly developed measurements of resilience, and described how demographic, physiological, behavioural, and social factors linked to resilience in this wild population.

As mentioned above, the framework of resilience can now be applied to address new research questions in wild animals. For example, it can be used to explore which individuals are more resilient to natural perturbations, whether more resilient individuals are also more resilient to human disturbances, and whether early-life adversities, e.g. through natural or human perturbations, are linked to later-in-life resilience to similar or different challenges. Therefore, this thesis provides an important starting point in the study of inter-individual differences in resilience, and of how and why individuals might differ in their ability to cope with stressful experiences.

Appendix I

Appendix I – I Permissions

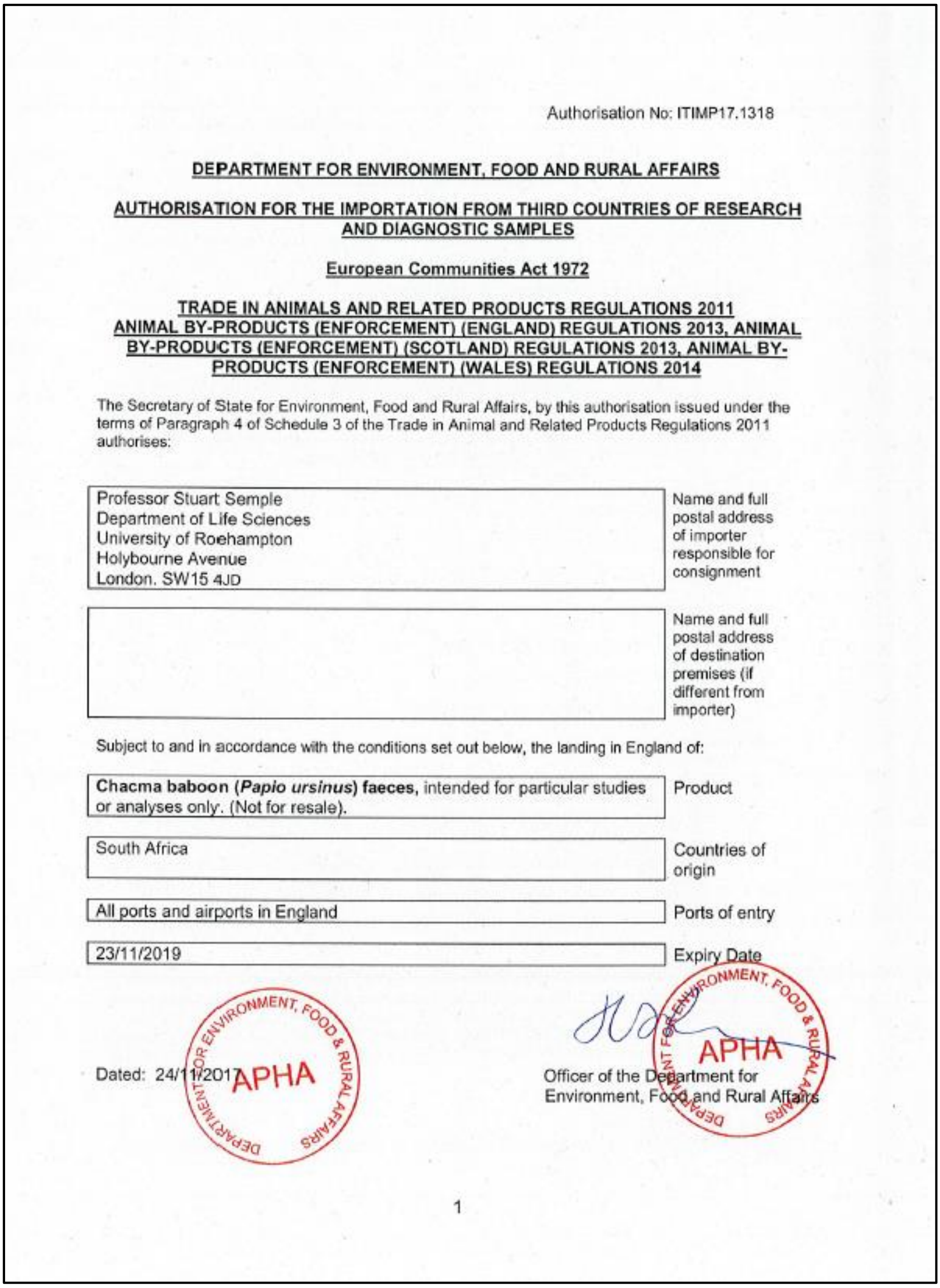
Page no.	Type of work	Name of work	Source of work	Copyright holder and contact	Permission requested on	I have permission yes /no	Permission note
32	figure	Figure 1.1	Hau, M., Casagrande, S., Ouyang, J.Q., Baugh, A.T., 2016. Glucocorticoid-mediated phenotypes in vertebrates. Chapter 2, Advances in the Study of Behavior, vol. 48.	© Elsevier	16.03.20	yes	Written permission
38	figure	Figure 1.2	Romero, L.M., Dickens, M.J., Cyr, N.E., 2009. The Reactive Scope Model - a new model integrating homeostasis, allostasis, and stress. Hormones and Behavior vol. 55, p. 375-389.	© Elsevier	16.03.20	yes	Written permission
41	figure	Figure 1.3	MacLarnon, A.M., Sommer, V., Goffe, A.S., Higham, J.P., Lodge, E., Tkaczynski, P.J., Ross, C., 2015. Assessing adaptability and reactive scope: introducing a new measure and illustrating its use through a case study of environmental stress in forest-living baboons. General and Comparative Endocrinology, vol. 215, p. 10–24.	© Elsevier	16.03.20	yes	Written permission
76	figure	Figure 2.5	Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., Irwan, A.M., Agil, M., Widdig, A., Engelhardt, A., 2011. Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo-rating. Animal Behaviour, vol. 82, p. 911–921.	© Elsevier	16.03.20	yes	Written permission

Appendix I – II Ethical approval

The research for this project was submitted for ethics consideration under the reference LSC 16/162 in the Department of Life Sciences and was approved under the procedures of the University of Roehampton's Ethics Committee on 23.08.2016.

Appendix I – III DEFRA import licence

Authorisation to import the freeze-dried faecal samples into the UK was given by the Department for Environment, Food and Rural Affairs under certain import conditions on the 24.11.2017. For pictures of the import authorisation, attached conditions, and attestation of subject health see below.



Authorisation No: ITIMP17.1318

DEPARTMENT FOR ENVIRONMENT, FOOD AND RURAL AFFAIRS

AUTHORISATION FOR THE IMPORTATION FROM THIRD COUNTRIES OF RESEARCH AND DIAGNOSTIC SAMPLES

European Communities Act 1972

TRADE IN ANIMALS AND RELATED PRODUCTS REGULATIONS 2011 ANIMAL BY-PRODUCTS (ENFORCEMENT) (ENGLAND) REGULATIONS 2013, ANIMAL BY-PRODUCTS (ENFORCEMENT) (SCOTLAND) REGULATIONS 2013, ANIMAL BY-PRODUCTS (ENFORCEMENT) (WALES) REGULATIONS 2014

The Secretary of State for Environment, Food and Rural Affairs, by this authorisation issued under the terms of Paragraph 4 of Schedule 3 of the Trade in Animal and Related Products Regulations 2011 authorises:

Professor Stuart Semple Department of Life Sciences University of Roehampton Holybourne Avenue London. SW15 4JD	Name and full postal address of importer responsible for consignment
	Name and full postal address of destination premises (if different from importer)

Subject to and in accordance with the conditions set out below, the landing in England of:

Chacma baboon (*Papio ursinus*) faeces, intended for particular studies or analyses only. (Not for resale).	Product
South Africa	Countries of origin
All ports and airports in England	Ports of entry
23/11/2019	Expiry Date

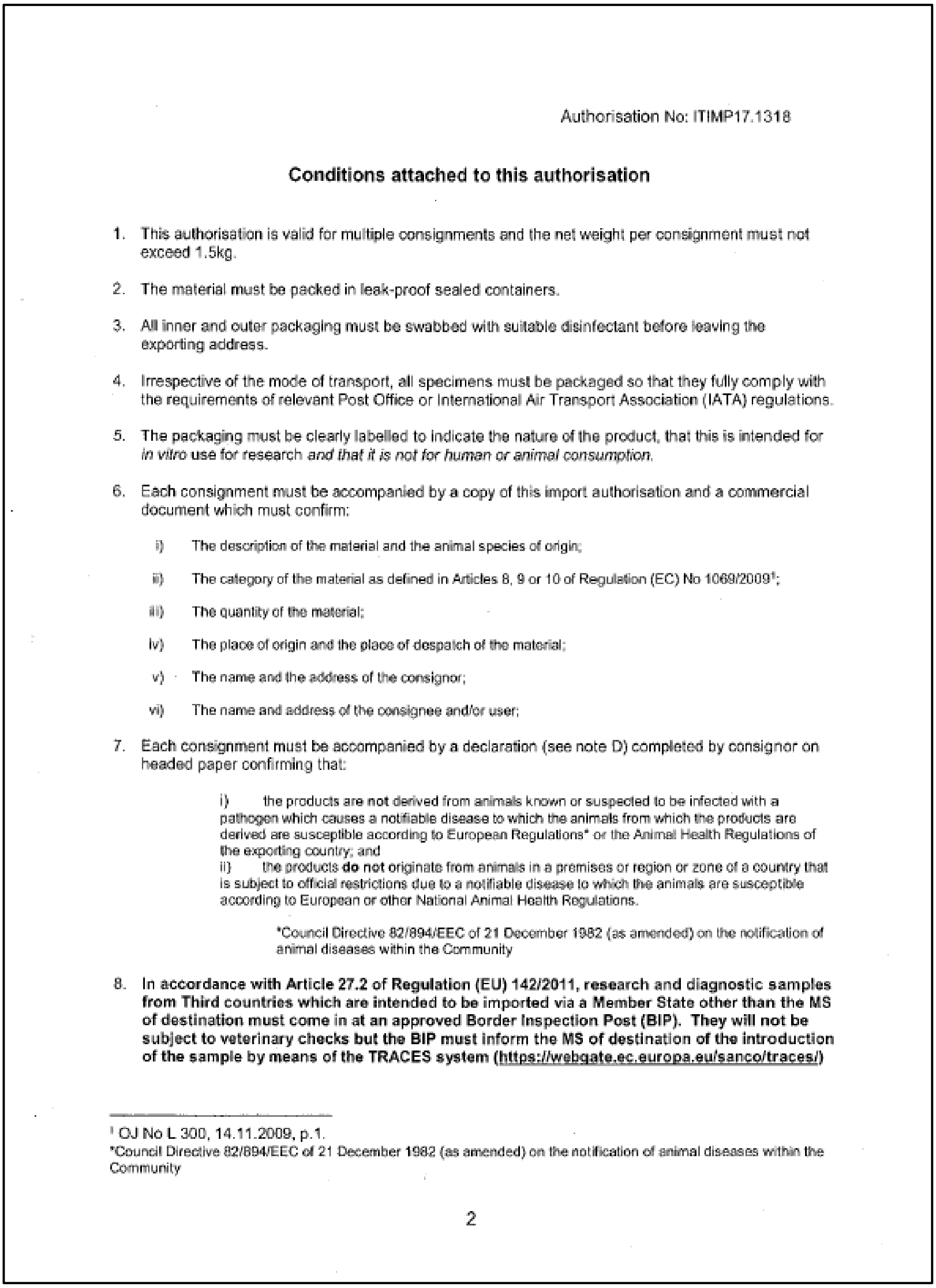
Dated: 24/11/2017

APHA

Officer of the Department for Environment, Food and Rural Affairs

APHA

1



Authorisation No: ITIMP17.1318

Conditions attached to this authorisation

1. This authorisation is valid for multiple consignments and the net weight per consignment must not exceed 1.5kg.
2. The material must be packed in leak-proof sealed containers.
3. All inner and outer packaging must be swabbed with suitable disinfectant before leaving the exporting address.
4. Irrespective of the mode of transport, all specimens must be packaged so that they fully comply with the requirements of relevant Post Office or International Air Transport Association (IATA) regulations.
5. The packaging must be clearly labelled to indicate the nature of the product, that this is intended for *in vitro* use for research *and that it is not for human or animal consumption.*
6. Each consignment must be accompanied by a copy of this import authorisation and a commercial document which must confirm:
    - i) The description of the material and the animal species of origin;
    - ii) The category of the material as defined in Articles 8, 9 or 10 of Regulation (EC) No 1069/2009[1];
    - iii) The quantity of the material;
    - iv) The place of origin and the place of despatch of the material;
    - v) The name and the address of the consignor;
    - vi) The name and address of the consignee and/or user;
7. Each consignment must be accompanied by a declaration (see note D) completed by consignor on headed paper confirming that:

    i) the products are **not** derived from animals known or suspected to be infected with a pathogen which causes a notifiable disease to which the animals from which the products are derived are susceptible according to European Regulations* or the Animal Health Regulations of the exporting country; and
    ii) the products **do not** originate from animals in a premises or region or zone of a country that is subject to official restrictions due to a notifiable disease to which the animals are susceptible according to European or other National Animal Health Regulations.

    *Council Directive 82/894/EEC of 21 December 1982 (as amended) on the notification of animal diseases within the Community

8. **In accordance with Article 27.2 of Regulation (EU) 142/2011, research and diagnostic samples from Third countries which are intended to be imported via a Member State other than the MS of destination must come in at an approved Border Inspection Post (BIP). They will not be subject to veterinary checks but the BIP must inform the MS of destination of the introduction of the sample by means of the TRACES system (https://webgate.ec.europa.eu/sanco/traces/)**

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[1] OJ No L 300, 14.11.2009, p.1.

*Council Directive 82/894/EEC of 21 December 1982 (as amended) on the notification of animal diseases within the Community

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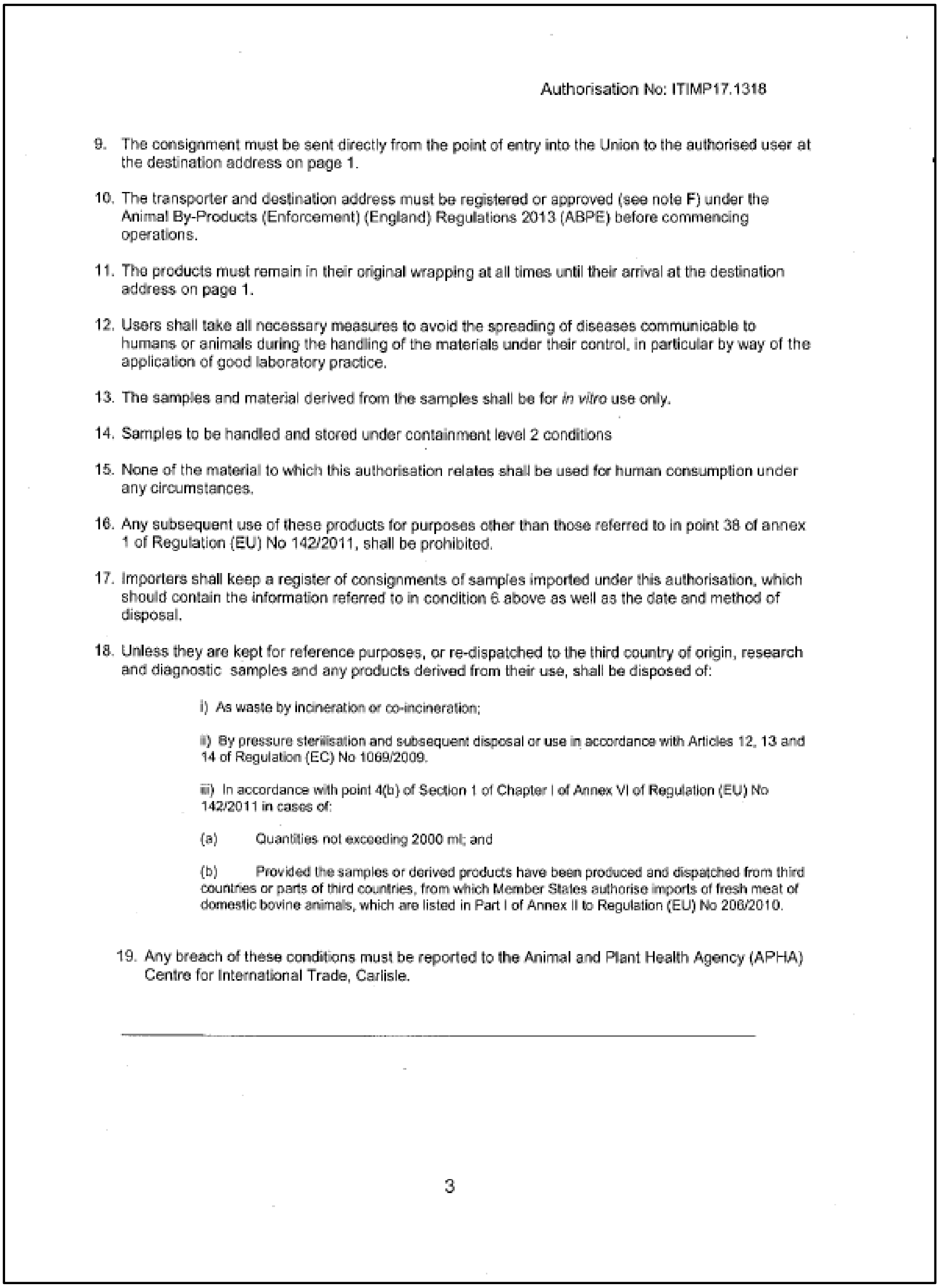


Authorisation No: ITIMP17.1318

9. The consignment must be sent directly from the point of entry into the Union to the authorised user at the destination address on page 1.

10. The transporter and destination address must be registered or approved (see note **F**) under the Animal By-Products (Enforcement) (England) Regulations 2013 (ABPE) before commencing operations.

11. The products must remain in their original wrapping at all times until their arrival at the destination address on page 1.

12. Users shall take all necessary measures to avoid the spreading of diseases communicable to humans or animals during the handling of the materials under their control, in particular by way of the application of good laboratory practice.

13. The samples and material derived from the samples shall be for *in vitro* use only.

14. Samples to be handled and stored under containment level 2 conditions

15. None of the material to which this authorisation relates shall be used for human consumption under any circumstances.

16. Any subsequent use of these products for purposes other than those referred to in point 38 of annex 1 of Regulation (EU) No 142/2011, shall be prohibited.

17. Importers shall keep a register of consignments of samples imported under this authorisation, which should contain the information referred to in condition 6 above as well as the date and method of disposal.

18. Unless they are kept for reference purposes, or re-dispatched to the third country of origin, research and diagnostic samples and any products derived from their use, shall be disposed of:

    i) As waste by incineration or co-incineration;

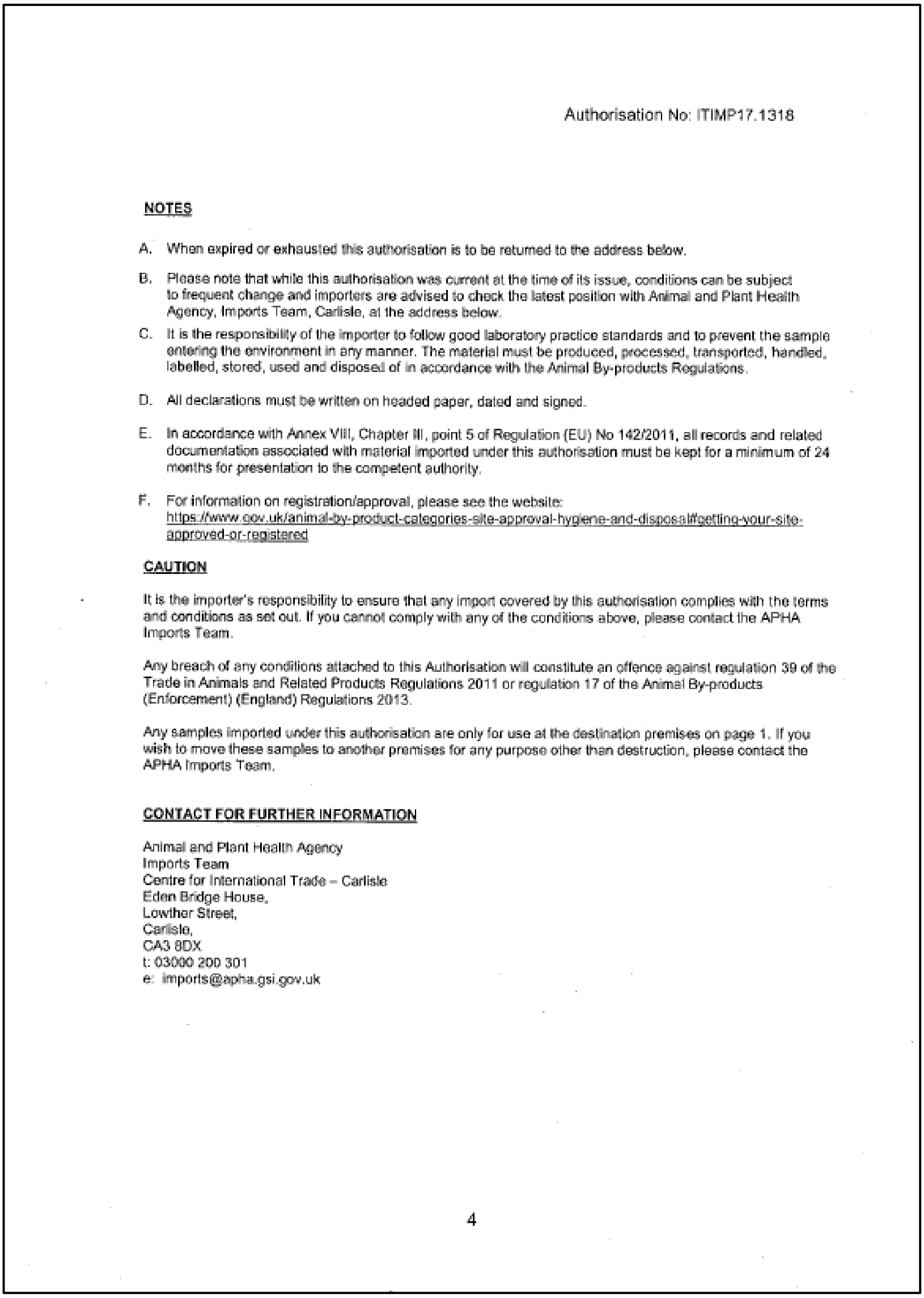
    ii) By pressure sterilisation and subsequent disposal or use in accordance with Articles 12, 13 and 14 of Regulation (EC) No 1069/2009.

    iii) In accordance with point 4(b) of Section 1 of Chapter I of Annex VI of Regulation (EU) No 142/2011 in cases of:

    (a) Quantities not exceeding 2000 ml; and

    (b) Provided the samples or derived products have been produced and dispatched from third countries or parts of third countries, from which Member States authorise imports of fresh meat of domestic bovine animals, which are listed in Part I of Annex II to Regulation (EU) No 206/2010.

19. Any breach of these conditions must be reported to the Animal and Plant Health Agency (APHA) Centre for International Trade, Carlisle.



Authorisation No: ITIMP17.1318

NOTES

A. When expired or exhausted this authorisation is to be returned to the address below.

B. Please note that while this authorisation was current at the time of its issue, conditions can be subject to frequent change and importers are advised to check the latest position with Animal and Plant Health Agency, Imports Team, Carlisle, at the address below.

C. It is the responsibility of the importer to follow good laboratory practice standards and to prevent the sample entering the environment in any manner. The material must be produced, processed, transported, handled, labelled, stored, used and disposed of in accordance with the Animal By-products Regulations.

D. All declarations must be written on headed paper, dated and signed.

E. In accordance with Annex VIII, Chapter III, point 5 of Regulation (EU) No 142/2011, all records and related documentation associated with material imported under this authorisation must be kept for a minimum of 24 months for presentation to the competent authority.

F. For information on registration/approval, please see the website:
https://www.gov.uk/animal-by-product-categories-site-approval-hygiene-and-disposal#getting-your-site-approved-or-registered

CAUTION

It is the importer's responsibility to ensure that any import covered by this authorisation complies with the terms and conditions as set out. If you cannot comply with any of the conditions above, please contact the APHA Imports Team.

Any breach of any conditions attached to this Authorisation will constitute an offence against regulation 39 of the Trade in Animals and Related Products Regulations 2011 or regulation 17 of the Animal By-products (Enforcement) (England) Regulations 2013.

Any samples imported under this authorisation are only for use at the destination premises on page 1. If you wish to move these samples to another premises for any purpose other than destruction, please contact the APHA Imports Team.

CONTACT FOR FURTHER INFORMATION

Animal and Plant Health Agency
Imports Team
Centre for International Trade – Carlisle
Eden Bridge House,
Lowther Street,
Carlisle,
CA3 8DX
t: 03000 200 301
e: imports@apha.gsi.gov.uk

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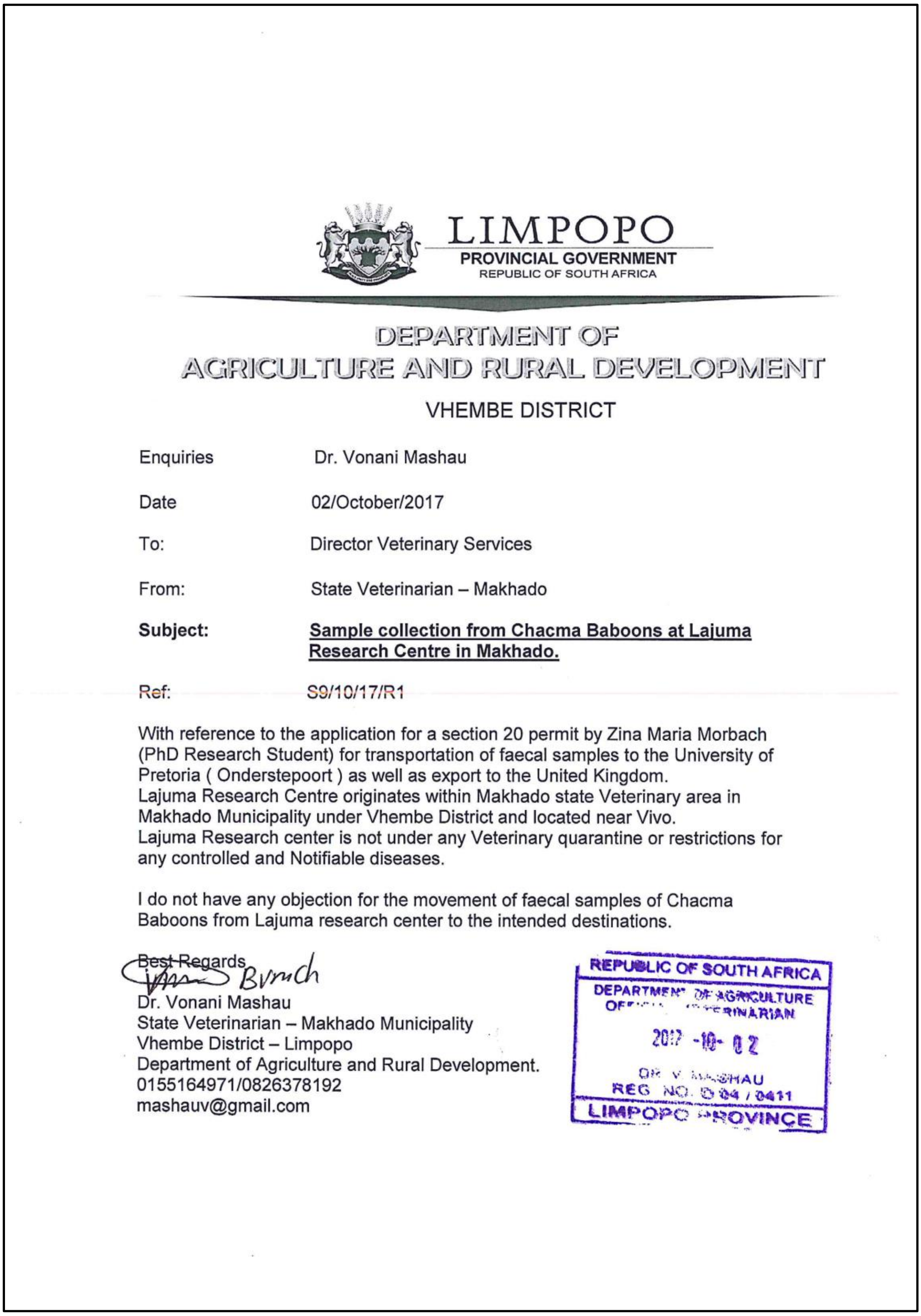

LIMPOPO
PROVINCIAL GOVERNMENT
REPUBLIC OF SOUTH AFRICA

DEPARTMENT OF
AGRICULTURE AND RURAL DEVELOPMENT

VHEMBE DISTRICT

Enquiries	Dr. Vonani Mashau
Date	02/October/2017
To:	Director Veterinary Services
From:	State Veterinarian – Makhado
Subject:	**<u>Sample collection from Chacma Baboons at Lajuma Research Centre in Makhado.</u>**
Ref:	S9/10/17/R1

With reference to the application for a section 20 permit by Zina Maria Morbach (PhD Research Student) for transportation of faecal samples to the University of Pretoria (Onderstepoort) as well as export to the United Kingdom.
Lajuma Research Centre originates within Makhado state Veterinary area in Makhado Municipality under Vhembe District and located near Vivo.
Lajuma Research center is not under any Veterinary quarantine or restrictions for any controlled and Notifiable diseases.

I do not have any objection for the movement of faecal samples of Chacma Baboons from Lajuma research center to the intended destinations.

Best Regards

Dr. Vonani Mashau
State Veterinarian – Makhado Municipality
Vhembe District – Limpopo
Department of Agriculture and Rural Development.
0155164971/0826378192
mashauv@gmail.com

REPUBLIC OF SOUTH AFRICA
DEPARTMENT OF AGRICULTURE
OFFICIAL VETERINARIAN
2017 -10- 02
DR V MASHAU
REG NO. D04/0411
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Appendix II

Appendix II – I Ethograms

Table A II-I 1 Ethogram of behaviours recorded during continuous and ad libitum sampling (bouts as defined in Duboscq et al., 2016; agonistic behaviours based on Kitchen et al., 2003; Ellis et al., 2011; self-directed behaviours based on Ellis et al., 2011).

General behaviour	
Approach	Walking into the close proximity (</= 1.5m) of an individual
Arrive together	Arriving in the close proximity (</= 1.5m) of another individual, when it is unclear who approached whom
Leave	Leaving the close proximity (</= 1.5m) of another individual
Leave each other	Leaving the close proximity (</= 1.5m) of another individual, when it is unclear who leaves whom
Walk by	Entering and leaving close proximity (</= 1.5m) within a few seconds, without looking at the other individual or any other obvious interaction
Infant carrying	Carrying an infant, either under the belly or on the back while walking, or holding it in the lap while sitting
Handle infant	Moving or manipulating some part of an infant rather than just touching or holding it
Pulling infant	Grabbing and pulling another individual's infant
Access infant	Trying to get access to another individual's infant; access can be granted or denied
Mating	An adult/adolescent male mounting an adult/adolescent female; with penetration and mating vocalisation from female
Play	Rough-and-tumble play, e.g. playfully chasing, biting, grabbing another individual, while showing playface
Affiliative behaviour	
Body contact	Moving into contact with another individual with any part of the body, for a minimum of 5 sec; if there is a break of >5 seconds it is counted as a new bout
Body both	Being in body contact with another individual for a minimum of 5 seconds; the instigator being unclear
Brush	Brushing past another individual while walking or standing; duration shorter than 5 seconds
Touch body	Touch another individual with the hand, while otherwise not being in body contact
Embrace	Put arm around another individual
Groom present	Animal presents its trunk or broadside; if seated or lying, trunk often presented with arm or leg up and head lifted and tilted
Grooming	Go through the fur of another individual with hands or mouth; if there is a break of >5 seconds it is counted as a new bout
Lip smacking	Make a rapid chattering noise with lips and teeth towards another individual
Come hither face	Combination of pulling up eyebrows, set back ears, and lip smacking towards another individual
Flex arms	Arms of animal flexed, lowering front half of body with rear in the air while looking at another individual; often accompanied by lip smacking and cocking of head (often inviting gesture to infant, pacifying to mother)
Grunting	Making grunting noises towards another individual, or group of individuals
Mounting	Mounting another individual without penetration
Genital touch	Touching another individual's genitals, e.g. during a greeting
Pelvis grab	One individual grabs another by the pelvis/hip, pulls them close; might be followed by mount, can be in combination with present, or while inspecting anogenital region
Inspect	Inspecting the anogenital region/swelling of another individual with nose/eyes/hands
Agonistic behaviour	
Agonism	Recorded once with every new agonistic interaction (i.e. either different interaction partner, or break of minimum 10 seconds)
Make room	Avoiding behaviour, moving away with part of body from another individual without leaving
Fear scream	Individual shows fear grimace (i.e. lips being pulled back over clenched teeth), or produces fear geck or fear scream towards another individual

Displace	Actively (staring etc. included) or passively (by walking by) displacing another individual, i.e. the interaction partner leaves the place it was in; modifier 1: dyadic/polyadic; modifier 2: active/passive
Present	Present posterior to another individual, can be both submissive or sexual. Modifier: engage (i.e. then followed by inspect/mount etc.) or ignore (no further response recorded)
Stare	Keep fixed gaze on another individual, while body is rigid
Ignore stare	Being stared at by another individual, but not moving away and not staring back
Lunge	Move towards another individual in a threat without moving more than 5m
Chase	Rapid running towards another individual with repeated change of direction, tracking the other animal, and not accompanied by gestures of fear or submission; that the other individual is fleeing is included, so not recorded additionally
Bite	Bite another individual as part of an agonistic interaction
Grab	Grab or try to grab another individual as part of an agonistic interaction (grab and slap were difficult to differentiate, so always recorded as grab)
Hold down	Grab or bite another individual and hold it down to the ground
Self-directed behaviour (= displacement behaviour)	
Scratching	Moving fingers/nails across any body part quickly; if break of 3 seconds or new body part, counted as a new scratch
Yawning with teeth	Yawning with lips pulled back over teeth
Yawning	Yawning with lips covering teeth
Auto-grooming	Combing through the own fur with hands or mouth; if break of 5 seconds, counted as a new bout
Genital manipulation	Manipulating own genitals with hands
Body shake	Shaking the whole body, often seen when wet
Tree shake	Standing on a branch or fallen tree and using body weight to shake it

Table A II-I 2 Categories of postures, activities, and proximities of conspecifics recorded during instantaneous data collection, which was conducted once a minute during focal animal observations.

Posture	**Activity**	**Proximity**
Lying	Resting	Body contact
Sitting	Feeding	Close radius (</= 1.5 m)
Standing	Foraging	Wider radius (> 1.5 m, <= 2.5 m)
Walking	Being Social	
Running	Traveling	
Climbing		
Jumping		

Appendix II – II Social network analysis

Table A II-II 1 Details on SNA metric calculations used (AF = affiliation network, AG = agonism network).

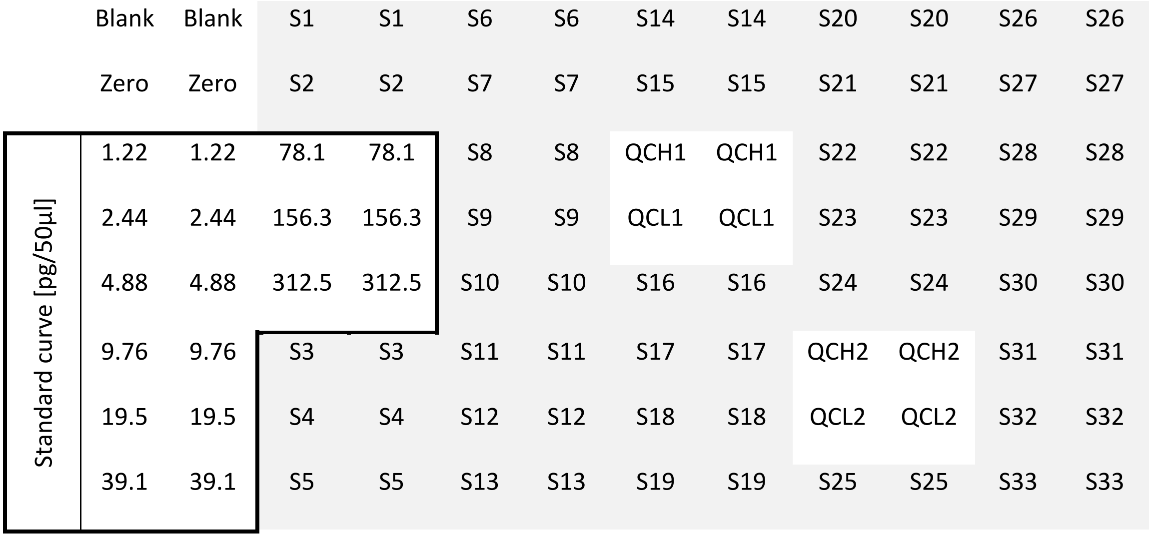
Package	**Metric**	**Weighted / unweighted**	**All edges / conditional edges**	**Code**
--	Strength	Weighted	CSI: All edges AG: All edges	rowSum(nw)
igraph	Degree	Unweighted	CSI: not calculated AG: All edges	degree(nw)
	Eigenvector centrality	Weighted (uses weights from nw)	CSI: All edges AG: All edges	evcent(nw, weights=NULL)$vector
	Individual clustering coefficient	Weighted (uses weights from nw, after Barrat et al., 2004)	CSI: Edges > 1 AG: All edges	transitivity(nw, type = "weighted")
tnet	Betweenness centrality	Weighted	CSI: All edges AG: All edges	betweenness_w(mtr, directed = F, alpha = 0.5)[,2]

--	Reach (for k = 2 steps) (code from http://www.shizukalab.com/toolkits/sna/node-level-calculations)	Unweighted	CSI: Edges > 1 AG: Edges ≥ mean	

```
# create function:
reach2=function(x){
  r=vector(length=vcount(x))
  for (i in 1:vcount(x)){
    n=neighborhood(x,2,nodes=i)
    ni=unlist(n)
    l=length(ni)
    r[i]=(l)/vcount(x)}
  r}
# use function:
reach2(nw)
```

Appendix II – III EIA procedures

Plates used for EIA consisted of 48 duplicate 50µl wells, which were coated with anti-rabbit immunoglobulin G, developed in sheep. Assay buffer for blanks and zeros, standard curve dilutions, quality controls (QCs), and samples were pipetted into the appropriate wells; for the layout of plates see Figure A II-III 1. Biotin-labelled steroid was added to all wells, and steroid specific antibodies were dispensed into all wells besides the blank; for details on the reagents added see Table A II-III 1. Plates were then incubated at 4°C overnight. After incubation, plates were washed and streptavidin-horseradish-peroxidase was added, an enzyme which binds to the biotin on the labelled steroids. Plates were incubated for 30 minutes on a shaker at room temperature and then washed again. Tetramethylbenzidine (TMB, the substrate) was added to all wells and plates were incubated on a shaker at room temperature in the dark until the zero wells gave a blue colour equivalent to an optical density of approximately 1.0 (between 30 and 60 minutes), as a result of the interaction between TMB and the peroxidase. To stop the reaction, 2M Sulphuric acid was dispensed into all wells, which turns the enzyme-biotin-labelled antigens yellow. Optical densities were read using a plate spectrophotometer at a wavelength of 450nm, using Ascent software.



	Blank	Blank	S1	S1	S6	S6	S14	S14	S20	S20	S26	S26
	Zero	Zero	S2	S2	S7	S7	S15	S15	S21	S21	S27	S27
Standard curve [pg/50µl]	1.22	1.22	78.1	78.1	S8	S8	QCH1	QCH1	S22	S22	S28	S28
	2.44	2.44	156.3	156.3	S9	S9	QCL1	QCL1	S23	S23	S29	S29
	4.88	4.88	312.5	312.5	S10	S10	S16	S16	S24	S24	S30	S30
	9.76	9.76	S3	S3	S11	S11	S17	S17	QCH2	QCH2	S31	S31
	19.5	19.5	S4	S4	S12	S12	S18	S18	QCL2	QCL2	S32	S32
	39.1	39.1	S5	S5	S13	S13	S19	S19	S25	S25	S33	S33

Figure A II-III 1 Microtiter layout containing blanks, zeros, standard curve concentrations [pg/50µl], QC High [39.1pg/50µl] and QC Low [9.76pg/50µl], with the remaining duplicates containing samples (S1-S33).

Table A II-III 1 Volumes of reagents added to all wells [µl].

	Assay buffer	**Standard/QC/Sample**	**Biotin-labelled steroid**	**Antibodies**
Blank	100	0	50	0
Zero	50	0	50	50
Standard curve	0	50	50	50
QCH/QCL	0	50	50	50
Samples	0	50	50	50

Appendix III – Physiological stress response levels and stress reactivity

Appendix III – I Demographic factors

Table A III-I 1 Details on the full and null LMM regarding females' fGCM concentrations, using their reproductive state at the time as predictor. Models included maximum daily temperature, rain/day, rain/month, age, and rank category. Individual ID was included as random factor. fGCM values were log$_{10}$-transformed to comply with model assumptions.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2	Cond. R^2
full model:					-12.06	0	0.925	14.37%	23.77%
Intercept	3.72	0.13	3.46, 3.98	<.0001					
lactating - cycling	**0.16**	**0.06**	**0.04, 0.29**	**.013**					
cycling - pregnant	-0.04	0.06	-0.16, 0.07	.48					
lactating - pregnant	**0.11**	**0.04**	**0.03, 0.20**	**.010**					
max. temperature	**-0.01**	**0.003**	**-0.02, -0.004**	**.001**					
rain/day	0.002	0.01	-0.01, 0.01	.615					
rain/month	-0.0002	0.0004	-0.001, 0.001	.501					
age	-0.05	0.03	-0.11, 0.01	.084					
rank	**-0.07**	**0.03**	**-0.13, -0.01**	**.022**					
null model:					-7.04	5.02	0.075	8.18%	17.87%
Intercept	3.72	0.13	3.45, 3.97	<.0001					
max. temperature	**-0.01**	**.004**	**-0.02, -0.01**	**.001**					
rain/day	0.002	.01	-0.01, 0.01	.727					
rain/month	-0.0001	.0004	-0.001, 0.001	.806					
age	-0.04	0.03	-0.10, 0.01	.135					
rank	-0.05	0.03	-0.11, 0.01	.076					

Table A III-I 2 Details on the full and null LMs regarding males' mean fGCM concentrations, using their dominance rank position, either measured as rank category or mean randomised Elo-rating, as predictor. Models included age.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2
full model:					167.24	2.82	0.171	20.99%
Intercept	2282.76	263.80	1674.44, 2891.09	<.0001				
rank category	-166.95	1.40	-441.26, 107.37	.198				
age	-8.19	94.18	-225.38, 209	.933				
full model:					167.75	3.33	0.132	17.84%
Intercept	1536.81	473.82	444.17, 2629.45	.012				
rand. Elo	0.42	0.34	-0.37, 1.22	.253				
age	-24.8	92.81	-238.82, 189.22	.796				
null model:					164.42	0	0.697	5.84%
Intercept	2057.26	220.20	1559.13, 2555.39	<.0001				
age	-69.24	87.92	-268.13, 129.65	.451				

Table A III-I 3 Details on the full and null LMs regarding males' demonstrated reactive scope measured as DRS, using their dominance rank position, either measured as rank category or mean randomised Elo-rating, as predictor. Models included age.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2
full model:					149.14	3.9	0.106	32.80%
Intercept	-57.16	115.90	-324.42, 210.09	.635				
rank category	53.04	52.26	-67.47, 173.56	.340				
age	52.62	41.38	-42.79, 148.04	.239				
full model:					148.49	3.25	0.147	36.18%
Intercept	236.01	197.43	-219.27, 691.29	.266				
rand. Elo	-0.18	0.14	-0.51, 0.15	.244				
age	53.11	38.67	-36.07, 142.28	.207				

null model:					145.24	0	0.747	27.74%
Intercept	14.48	92.07	-193.8, 222.77	.879				
age	72.02	36.76	-11.14, 155.18	.082				

Table A III-I 4 Details on the full and null LMs regarding males' demonstrated reactive scope measured as DRS_{CV}, using their dominance rank position, either measured as rank category or mean randomised Elo-rating, as predictor. Models included age.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	ω	Marginal R^2
full model:					18.07	4.97	0.069	9.11%
Intercept	0.31	0.3	-0.38, 1.00	.331				
rank category	0.06	0.14	-0.25, 0.37	.667				
age	0.06	0.11	-0.18, 0.31	.572				
full model:					17.19	4.09	0.107	14.89%
Intercept	0.81	0.51	-0.35, 1.98,	.146				
rand. Elo	-0.0003	0.0004	-0.001, 0.001	.376				
age	0.05	0.1	-0.18, 0.28	.634				
null model:					13.1	0	0.825	8.11%
Intercept	0.39	0.23	-0.12, 0.90	.119				
age	0.09	0.09	-0.12, 0.29	.372				

Table A III-I 5 Details on the full and null LMs regarding females' mean fGCM concentrations, using their dominance rank position, either measured as rank category or mean randomised Elo-rating, as predictor. Models included age.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	ω	Marginal R^2
full model:					278.34	0	0.530	37.69%
Intercept	2959.14	304.65	2313.31, 3604.98	<.0001				
rank category	**-262.65**	**85.58**	**-444.06, -81.24**	**.007**				
age	-147.11	88.58	-334.89, 40.67	.116				
full model:					280.46	2.12	0.184	30.89%
Intercept	1530.81	321.56	849.13, 2212.49	.0002				
rand. Elo	**0.74**	**0.29**	**0.14, 1.35**	**.02**				
age	-150.44	94.16	-350.04, 49.17	.13				
null model:					283.88	5.54	0.033	5.17%
Intercept	2204.0	219.7	1740.46, 2667.57	<.0001				
age	-106.1	107.1	-331.98, 119.84	.336				

Table A III-I 6 Details on the full and null LMs regarding females' demonstrated reactive scope measured as DRS, using their dominance rank position, either measured as rank category or mean randomised Elo-rating, as predictor. Models included age. DRS values were $\log_2$-transformed to comply with model assumptions.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	ω	Marginal R^2
full model:					72.69	3.25	0.122	0.28%
Intercept	7.93	1.36	5.05, 10.82	<.0001				
rank category	-0.02	0.38	-0.83, 0.79	.965				
age	0.08	0.4	-0.76, 0.92	.836				
full model:					72.66	3.22	0.124	0.42%
Intercept	7.71	1.36	4.83, 1.58	<.0001				
rand. Elo	0.0002	0.001	-0.002, 0.003	.872				
age	0.07	0.4	-0.77, 0.92	.854				
null model:					69.44	0	0.622	0.29%
Intercept	7.89	0.78	6.24, 9.53	<.0001				
age	0.09	0.38	-0.71, 0.89	.823				

Table A III-I 7 Details on the full and null LMs regarding females' demonstrated reactive scope measured as DRS_{CV}, using their dominance rank position, either measured as rank category or mean randomised Elo-rating, as predictor. Models included age. DRS_{CV} values were $\log_2$-transformed to enhance comparability.

Fixed effect	estimate	SE	95%-CI	p-value	AICC	Δ AICC	ω	Marginal R2
full model:					47.59	3.14	0.130	7.11%
Intercept	-0.96	0.70	-2.45, 0.53	.190				
rank category	0.06	0.2	-0.35, 0.48	.751				
age	0.24	0.20	-0.2, 0.67	.261				

full model:					47.69	3.24	0.124	6.69%
Intercept	-0.7	0.70	-2.19, 0.79	.337				
rand. Elo	-0.0001	0.001	-0.001, 0.001	.885				
age	0.23	0.21	-0.20, 0.67	.273				
null model:					44.45	0	0.623	6.96%
Intercept	-0.78	0.40	-1.63, 0.07	.070				
age	0.23	0.2	-0.19, 0.64	.262				

Appendix III – II Environmental factors

Table A III-II 1 Details on the full and null LMMs regarding males' fGCM concentrations, using weather variables as predictors. Full models included either maximum or minimum daily temperature, as well as rain/day, rain/month, age, and rank category. Null model included age and rank category. Individual ID was included as random factor. fGCM values were $\log_{10}$-transformed to comply with model assumptions.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	**ω**	Marginal R^2	Cond. R^2
full model:					-95.75	4.55	0.092	10.97%	13.11%
Intercept	3.51	0.08	3.34, 3.67	<.0001					
max. temp	**-0.01**	**0.003**	**-0.01, -0.002**	**.010**					
rain/day	0.01	0.004	-0.002, 0.02	.128					
rain/month	-0.0004	0.0003	-0.001, 0.0003	.258					
age	-0.01	0.02	-0.05, 0.03	.674					
rank	-0.03	0.02	-0.08, 0.01	.148					
full model:					-100.31	0	0.897	14.06%	17.41%
Intercept	3.53	0.08	3.38, 3.68	<.0001					
min. temp	**-0.02**	**0.01**	**-0.03, -0.01**	**.0008**					
rain/day	0.01	0.004	-0.001, 0.02	.078					
rain/month	-0.00003	0.0004	-0.001, 0.001	.920					
age	-0.01	0.02	-0.04, 0.03	.802					
rank	-0.03	0.02	-0.08, 0.01	.152					
null model:					-91.57	8.74	0.011	3.36%	5.8%
Intercept	3.31	0.05	3.21, 3.42	<.0001					
age	-0.01	0.02	-0.04, 0.03	.791					
rank	-0.03	0.02	-0.08, 0.01	.142					

Table A III-II 2 Details on the full and null LMMs regarding females' fGCM concentrations, using weather variables as predictors. Full models included either maximum or minimum daily temperature, as well as rain/day, rain/month, age, and rank category, as well as reproductive state as categorical factor with lactating as reference category. Interaction models included an interaction term of the temperature measure and reproductive state. Null model included age, rank category, and reproductive state. Individual ID was included as random factor. fGCM values were $\log_{10}$-transformed to comply with model assumptions.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	**ω**	Marginal R^2	Cond. R^2
full model:					-12.06	0	0.645	14.38%	23.77%
Intercept	3.72	0.13	3.46, 3.98	<.0001					
max. temp	**-0.01**	**0.003**	**-0.02, -0.004**	**.001**					
rain/day	0.002	0.01	-0.01, 0.01	.615					
rain/month	-0.0002	0.0004	-0.001, 0.001	.501					
age	-0.05	0.03	-0.11, 0.01	.084					
rank	**-0.07**	**0.03**	**-0.13, -0.01**	**.022**					
reprod. (cycl)	**0.16**	**0.06**	**0.04, 0.29**	**.013**					
reprod. (preg)	**0.11**	**0.04**	**0.03, 0.20**	**.010**					

interact. model:					-9.55	2.51	0.184	15.16%	23.58%
Intercept	3.79	0.14	3.51, 4.07	<.0001					
max. temp	**-0.01**	**0.004**	**-0.02, -0.01**	**.001**					
max. temp*cycl	0.02	0.01	-0.01, 0.04	.166					
max. temp*preg	0.004	0.01	-0.01, 0.02	.61					
rain/day	0.002	0.01	-0.01, 0.01	.662					
rain/month	-0.0002	0.0004	-0.001, 0.001	.564					
age	-0.05	0.03	-0.11, 0.004	.071					
rank	**-0.07**	**0.03**	**-0.13, -0.01**	**.02**					
reprod. (cycl)	-0.22	0.28	-0.78, 0.33	.421					
reprod. (preg)	0.02	0.18	-0.35, 0.38	.911					
full model:					-2.89	9.17	0.007	10.9%	20.75%
Intercept	3.52	0.12	3.28, 3.77	<.0001					
min. temp	-0.01	0.01	-0.02, 0.01	.31					
rain/day	0.01	0.01	-0.004, 0.02	.230					
rain/month	-0.0004	0.0004	-0.001, 0.0004	.34					
age	-0.05	0.03	-0.10, 0.01	.128					
rank	**-0.07**	**0.03**	**-0.13, -0.01**	**.025**					
reprod. (cycl)	**0.17**	**0.06**	**0.04, 0.3**	**.009**					
reprod. (preg)	**0.11**	**0.04**	**0.03, 0.21**	**.012**					
interact. model:					-8.96	3.1	0.137	14.82%	21.88%
Intercept	3.66	0.12	3.41, 3.90	<.0001					
min. temp	**-0.02**	**0.01**	**-0.03, -0.01**	**.009**					
min. temp*cycl	**0.05**	**0.02**	**0.02, 0.08**	**.003**					
min. temp*preg	**0.03**	**0.01**	**0.001, 0.05**	**.039**					
rain/day	0.01	0.01	-0.002, 0.02	.153					
rain/month	-0.0004	0.0004	-0.001, 0.0004	.319					
age	-0.04	0.03	-0.09, 0.02	.184					
rank	**-0.07**	**0.03**	**-0.12, -0.01**	**.018**					
reprod. (cycl)	**-0.43**	**0.20**	**-0.83, -0.03**	**.034**					
reprod. (preg)	-0.2	0.15	-0.51, 0.12	.204					
null model:					-5.73	6.33	0.027	9.43%	18.93%
Intercept	3.43	0.1	3.22, 3.63	<.0001					
age	-0.04	0.03	-0.10, 0.02	.146					
rank	**-0.07**	**0.03**	**-0.12, -0.01**	**.036**					
reprod. (cycl)	**0.15**	**0.06**	**0.03, 0.28**	**.019**					
reprod. (preg)	**0.11**	**0.04**	**0.02, 0.20**	**.016**					

Table A III-II 3 Details on the full and null LMM regarding males' and females' change in fGCM concentrations in response to predation and disappearance events in period 1, compared to the mean level before the first event of the period, using the number of days since the first event as predictor. Models included rank category and sex, with females as reference category; age was significantly correlated with sex and thus excluded. Individual ID was included as random factor.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	ΔAIC_C	**ω**	Marginal R^2	Cond. R^2
full model:					463.34	0	0.946	25.61%	33.37%
Intercept	1389.41	516.61	671.27, 2414.46	.021					
days	-17.36	11.41	-42.44, 1.15	.14					
rank	-93.28	169.74	-399.57, 136.34	.575					
sex (m)	**-586.22**	**231.67**	**-1021.93, -252.69**	**.032**					
null model:					469.07	5.73	0.054	18.41%	33.14%
Intercept	1019.71	521.51	23.53, 2009.07	.077					
rank	-47.86	175.83	-382.48, 288.32	.791					
sex (m)	-560.09	256.12	-1045.03, -68.78	.054					

Table A III-II 4 Details on the full and null LMM regarding males’ and females’ change in fGCM concentrations in response to predation and disappearance events in period 2, compared to the mean level before the first event of the period, using the number of days since the first event as predictor. Models included rank category and sex, with females as reference category; age was significantly correlated with sex and thus excluded. Individual ID was included as random factor.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2	Cond. R^2
full model:					433.69	0	0.935	17.97%	57.01%
Intercept	-998.71	706.87	-2299.54, 300.69	.183					
days	-12.42	7.65	-28.18, 1.90	.118					
rank	356.25	225.59	-56.81, 772.45	.145					
sex (m)	133.50	335.3	-481.19, 751.00	.700					
null model:					439.02	5.33	0.065	11.56%	55.48%
Intercept	-1338.4	708.62	-2653.72, -24.98	.087					
rank	355.14	236.59	-83.42, 794.55	.163					
sex (m)	156.25	351.96	-496.17, 810.86	.667					

Table A III-II 5 Details on the full and null LMM regarding males’ fGCM concentrations in response to predation and disappearance events in period 1, compared to the effect of weather during this time period, using a ‘before vs after the predation event’ categorical factor. All models included maximum and minimum daily temperature, rain/day, rain/month, age, and rank category as fixed effects. Individual ID was included as random factor. fGCM values were log$_{10}$-transformed to comply with model assumptions.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2	Cond. R^2
full model:					-51.35	1.25	0.349	27.65%	27.65%
Intercept	3.66	0.2	3.27, 4.05	<.0001					
period (before)	-0.06	0.04	-0.14, 0.03	.175					
max. temperature	-0.01	0.01	-0.03, 0.01	.249					
min. temperature	-0.004	0.01	-0.03, 0.02	.685					
rain/day	-0.50	0.29	-1.07, 0.07	.087					
rain/month	0.01	0.01	-0.004, 0.02	.184					
age	0.002	0.02	-0.04, 0.04	.904					
rank	**-0.08**	**0.02**	**-0.12, -0.03**	**.0008**					
null model:					-52.6	0	0.651	24.92%	24.92%
Intercept	3.71	0.2	3.31, 4.10	<.0001					
max. temperature	-0.01	0.01	-0.03, 0.002	.091					
min. temperature	-0.002	0.01	-0.02, 0.02	.841					
rain/day	**-0.58**	**0.29**	**-1.15, -0.01**	**.049**					
rain/month	0.01	0.01	-0.01, 0.01	.314					
age	0.004	0.02	-0.04, 0.04	.825					
rank	**-0.07**	**0.02**	**-0.12, -0.03**	**.001**					

Table A III-II 6 Details on the full and null LMM regarding females' fGCM concentrations in response to predation and disappearance events in period 1, compared to the effect of weather during this time period, using a 'before vs after the predation event' categorical factor (with 'after' as reference category). All models included maximum and minimum daily temperature, rain/day, rain/month, age, rank category, and reproductive state at the time (with cycling as reference category) as fixed effects. Individual ID was included as random factor.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	ω	Marginal R^2	Cond. R^2
full model:					917.42	0	0.988	42.55%	58.37%
Intercept	4047.41	1285.57	1475.69, 6611.01	.003					
period (before)	**-772.89**	**210.44**	**-1196.09, -353.24**	**.001**					
max. temperature	-51.97	48.06	-151.07, 44.12	.285					
min. temperature	41.61	47.65	-20.30, 98.49	.387					
rain/day	-548.52	1493.31	-1618.85, 2074.36	.715					
rain/month	22.84	28.78	-15.71, 54.14	.432					
age	-132.02	163.85	-154.08, 113.99	.432					
rank	**-413.15**	**171.57**	**-500.21, -217.75**	**.025**					
reprod. (lact.)	175.36	413.57	111.67, 664.72	.678					
reprod. (preg.)	339.38	441.24	-73.37, 666.04	.456					
null model:					926.24	8.82	0.012	30.14%	47.8%
Intercept	4500.22	1421.6	1662.18, 7336.76	.003					
max. temperature	-83.56	53.02	-191.5, 22.16	.122					
min. temperature	94.36	50.9	12.35, 172.91	.071					
rain/day	-2173.21	1595.69	-5371.26, -3510.48	.181					
rain/month	-8.66	30.8	-70.39, 53.13	.78					
age	-133.44	179.03	-530.45, 225.34	.468					
rank	**-547.21**	**183.54**	**-930.54, -170.53**	**.008**					
reprod. (lact.)	78.8	449.9	-893.62, 1006.56	.864					
reprod. (preg.)	244.44	479.97	-754.1, 1276.72	.62					

Table A III-II 7 Details on the full and null LMMs regarding males' fGCM concentrations in response to predation and disappearance events in period 2, compared to the effect of weather during this time period, using a 'before vs after the predation event' categorical factor (with 'after' as reference category). Full models included either the categorical before vs after predation factor or rain/month. All models included minimum daily temperature, rain/day, age, and rank category as fixed effects. Individual ID was included as random factor.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	ω	Marginal R^2	Cond. R^2
full model:					940.13	0	0.510	23.21%	27.5%
Intercept	2117.26	458.62	1199.59, 3055.95	<.0001					
period (before)	**375.14**	**165.10**	**42.06, 714.04**	**.027**					
min. temperature	-46.88	29.74	−100.85, 12.91	.120					
rain/day	-206.09	319.11	−777.95, 419.21	.521					
age	-6.95	86.28	-151.11, 134.55	.937					
rank	-24.40	98.14	-173.59, 145.10	.809					
full model:					941.08	0.95	0.318	22.06%	26.74%
Intercept	2566.73	376.19	1817.09, 3335.27	<.0001					
rain/month	**-7.59**	**3.74**	**-15.18, -0.05**	**.047**					
min. temperature	-55.67	28.64	-109.39, -0.66	.057					
rain/day	-345.35	321.10	-985.86, 298.25	.287					
age	1.66	87.18	-184.34, 188.76	.985					
rank	-24.08	99.81	-250.55, 184.64	.815					
null model:					942.30	2.17	0.172	16.72%	24.22%
Intercept	2770.61	383.08	2003.66, 355.81	<.0001					
min. temperature	**-85.51**	**25.25**	**-135.84, -35.2**	**.0001**					
rain/day	-297.63	328.80	-955.93, 366.35	.369					
age	23.26	94.55	-181.95, 224.75	.810					
rank	-46.53	109.26	-291.66, 185.41	.68					

Table A III-II 8 Details on the full and null LMMs regarding females' fGCM concentrations in response to predation and disappearance events in period 2, compared to the effect of weather during this time period, using a 'before vs after the predation event' categorical factor (with 'after' as reference category). Full models included either the categorical before vs after predation factor or rain/month. All models included maximum and minimum daily temperature, rain/day, age, rank category, and reproductive state at the time (with cycling as reference category) as fixed effects. Individual ID was included as random factor.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2	Cond. R^2
full model:					1767.77	0	0.506	25.19%	41.17%
Intercept	2728.83	704.6	1310.93, 4127.86	.0002					
period (before)	**307.01**	**121.29**	**66.11, 551.73**	**.013**					
max. temperature	3.85	15.09	-26.28, 33.72	.799					
min. temperature	**-69.06**	**27.61**	**-123.93, -13.47**	**.014**					
rain/day	104.29	181.38	-254.29, 464.86	.567					
age	-215.44	107.03	-442.65, 9.6	.066					
rank	-217.2	112.16	-452.20, 15.41	.071					
reprod. (lact.)	386.97	358.64	-323.98, 1172.53	.287					
reprod. (preg.)	461.09	374.34	-289.61, 1205.54	.224					
full model:					1768.16	0.39	0.416	24.83%	41.97%
Intercept	3056.03	681.31	1666.99, 4405.35	<.0001					
rain/month	**-7.02**	**2.88**	**-12.76, -1.33**	**.016**					
max. temperature	6.46	15.34	-24.17, 36.83	.675					
min. temperature	**-72.32**	**27.37**	**-126.61, -17.41**	**.01**					
rain/day	39.72	176.49	-309.26, 389.84	.822					
age	-214.01	109.59	-446.80, 15.95	.073					
rank	-222.64	114.67	-462.17, 15.54	.07					
reprod. (lact.)	378.31	362.99	-342.57, 1179.64	.304					
reprod. (preg.)	425.24	378.9	-332.12, 1179.74	.267					
null model:					1771.49	3.72	0.079	21.69%	40.24%
Intercept	3297.71	695.24	1898.19, 4677.35	<.0001					
max. temperature	-3.83	15.09	-33.99, 26.05	.800					
min. temperature	**-87.92**	**27.29**	**-141.95, -33.47**	**.002**					
rain/day	-13.17	179.41	-368.01, 342.27	.942					
age	-204.10	113.89	-444.12, 32.33	.094					
rank	-208.60	118.92	-456.38, 35.53	.096					
reprod. (lact.)	375.51	374.87	-365.78, 1165.26	.322					
reprod. (preg.)	486.68	389.90	-293.20, 1260.92	.217					

Appendix IV – Coping behaviour and social buffering

Appendix IV – I Coping behaviour

PREDATION

Table A IV-I 1 Details on the full and null LMMs regarding males' changes in scratching rates after a predation event, using demonstrated reactive scope (DRS and DRS$_{CV}$), mean fGCM concentrations, and the dyadic CSI to the killed individual as predictors. Models included age, rank category, and predation event 1 or 2.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	ω	Marginal R^2	Cond. R^2
full model DRS:					178.03	4.83	0.055	26.96%	64.63%
Intercept	-25.16	17.76	-62.71, 11.76	.176					
DRS	-0.04	0.05	-0.16, 0.07	.409					
age	-1.39	6.37	-15.47, 12.75	.833					
rank category	13.10	7.24	-2.79, 29.07	.107					
pred. 2	0.52	6.12	-5.89, 22.44	.163					
full model DRS$_{CV}$: *****					178.71	5.51	0.039	22.30%	64.62%
Intercept	-21.34	20.36	-64.49, 21.73	.313	(161.32)	(2.92)		(42.58%)	
DRS$_{CV}$	-6.06	26.50	-65.79, 51.60	.825					
age	-3.73	6.42	-17.92, 1ß.53	.578					
rank category	11.88	7.61	-4.94, 28.55	.156					
pred. 2	9.65	6.12	-5.77, 22.60	.158					
full model fGCM:					175.05	1.85	0.244	8.81%	68.09%
Intercept	-38.67	46.23	-141.46, 58.41	.421					
mean fGCM	0.02	0.02	-0.03, 0.06	.493					
age	1.09	5.52	-10.94, 13.21	.847					
pred. 2	9.79	5.94	-4.70, 22.27	.138					
full model CSI:					178.36	5.16	0.047	22.36%	69.34%
Intercept	-19.83	19.06	-59.48, 20.35	.314					
CSI	-4.89	7.20	-19.79, 12.19	.511					
age	-4.24	5.7	-16.85, 8.33	.478					
rank category	12.54	7.68	-4.31, 29.4	.139					
pred. 2	8.00	6.42	-6.71, 21.96	.248					
null model:					173.20	0	0.615	22.05%	64.35%
Intercept	-23.46	18.12	-61.71, 14.28	.215	(158.4)	(0)		(24.35%)	
age	-4.49	5.51	-16.78, 7.62	.440					
rank category	12.25	7.44	-4.14, 28.61	.137					
pred. 2	9.60	6.14	-5.91, 22.57	.161					

*** jos influential point in DRS$_{CV}$ model** (AIC$_C$ and effect sizes of models without influential data point in brackets)

Table A IV-I 2 Details on the full LMM including DRS$_{CV}$ and null model without the influential data point regarding males' changes in scratching rates after a predation event. Models included age, rank category, and predation event 1 or 2.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	ω	Marginal R^2	Cond. R^2
full model:					161.32	2.92	0.188	42.58%	42.58%
Intercept	21.64	18.4	-18.38, 68.47	.257					
DRS$_{CV}$	**-59.55**	**27.00**	**-128.87, 1.09**	**.042**					
age	-3.98	4.34	-14.23, 6.67	.373					
rank category	6.37	5.70	-7.84, 19.17	.281					
pred. 2	8.37	7.34	-7.96, 24.70	.301					
null model:					158.4	0	0.812	24.35%	55.83%
Intercept	-7.95	15.97	-43.45, 28.03	.634					
age	-7.28	5.68	-20.43, 5.71	.254					
rank category	11.23	7.11	-4.94, 27.39	.167					
pred. 2	9.49	7.19	-9.71, 24.87	.243					

Table A IV-I 3 Details on the full and null LMMs regarding males' changes in their rates of all self-directed behaviours after a predation event, using demonstrated reactive scope (DRS and DRS$_{CV}$), mean fGCM concentrations, and the dyadic CSI to the killed individual as predictors. Models included age, rank category, and predation event 1 or 2.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2	Cond. R^2
full model DRS:					192.45	4.82	0.052	20.87%	41.14%
Intercept	-32.51	25.63	-86.08, 20.54	.221					
DRS	-0.06	0.07	-0.21, 0.09	.409					
age	-0.12	8.22	-18.34, 18.13	.988					
rank category	14.68	9.45	-5.96, 35.59	.157					
pred. 2	12.96	10.58	-11.9, 25.14	.256					
full model DRS$_{CV}$:					193.14	5.51	0.036	16.77%	40.95%
Intercept	-27.96	28.63	-87.90, 31.69	.343					
DRS$_{CV}$	.7.41	34.19	-85.16, 66.71	.834					
age	-3.22	8.27	-21.53, 15.21	.708					
rank category	13.21	9.93	-8.68, 24.96	.218					
pred. 2	13.18	10.61	-12.03, 35.53	.250					
full model fGCM:					188.95	1.32	0.296	8.34%	45.71%
Intercept	-50.13	60.13	-185.11, 74.78	.422					
mean fGCM	0.02	0.03	-0.04, 0.08	.512					
age	2.09	6.92	-13.02, 17.37	.770					
pred. 2	13.27	10.34	-11.55, 34.91	.234					
full model CSI:					192.91	5.28	0.041	17.52%	45.77%
Intercept	-25.99	27.39	-82.71, 31.02	.356					
CSI	-6.55	11.80	-31.02, 18.53	.588					
age	-2.83	7.28	-20.03, 12.26	.614					
rank category	14.13	9.94	-7.59, 36.02	.190					
pred. 2	10.98	11.13	-14.14, 24.80	.350					
null model:					187.63	0	0.575	16.52%	40.45%
Intercept	-30.51	26.1	-84.96, 23.5	.258					
age	-4.13	7.09	-20.07, 11.45	.577					
rank category	13.65	9.71	-7.65, 35.03	.196					
pred. 2	13.07	10.64	-12.19, 35.49	.255					

Table A IV-I 4 Details on the full and null LMMs regarding males' changes in their rates of giving grooming after a predation event, using demonstrated reactive scope (DRS and DRS$_{CV}$), mean fGCM concentrations, and the dyadic CSI to the killed individual as predictors. Models included age, rank category, and predation event 1 or 2.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2	Cond. R^2
full model DRS: *****					-16.59	18.89	0.000	21.20%	21.20%
Intercept	-0.05	0.08	-0.21, 0.11	.498	(-35.37)	(4.72)		(20.74%)	
DRS	0.0002	0.0001	-0.0001, 0.001	.232					
age	-0.01	0.02	-0.06, 0.04	.661					
rank category	-0.02	0.03	-0.07, 0.03	.470					
pred. 2	0.06	0.04	-0.02, 0.13	.132					
full model DRS$_{CV}$: *****					-15.75	19.73	0.000	17.27%	17.27%
Intercept	-0.08	0.08	-0.26, 0.09	.326	(-36.59)	(3.5)		(26.51%)	
DRS$_{CV}$	0.07	0.09	-0.12, 0.26	.434					
age	-0.003	0.02	-0.05, 0.04	.870					
rank category	-0.01	0.03	-0.07, 0.04	.685					
pred. 2	0.06	0.04	-0.02, 0.13	.146					
full model fGCM: *****					-20.42	15.06	0.001	12.87%	12.87%
Intercept	-0.05	0.16	-0.37, 0.28	.772	(-40.09)	(0)		(14.00%)	
mean fGCM	-0.00002	0.0001	-0.0001, 0.0001	.797					
age	-0.001	0.02	-0.04, 0.03	.934					
pred. 2	0.06	0.04	-0.02, 0.14	.141					
full model CSI:					-35.48	0	0.999	73.23%	73.23%
Intercept	0.02	0.05	-0.07, 0.12	.582	(-34.26)	(5.83)		(15.13%)	
CSI	**-0.13**	**0.02**	**-0.18, -0.09**	**<.0001**					
age	0.01	0.01	-0.01, 0.03	.296					
rank category	-0.003	0.02	-0.03, 0.03	.855					
pred. 2	0.01	0.02	-0.04, 0.06	.629					

null model:					-20.68 (-40.03)	14.8 (0.06)	0.001	14.18% (13.68%)	14.18%
Intercept	-0.06	0.08	-0.23, 0.10	.458					
age	0.01	0.02	-0.04, 0.05	.784					
rank category	-0.01	0.03	-0.07, 0.04	.572					
pred. 2	0.06	0.04	-0.02, 0.13	.145					

*** scf influential point in DRS_{CV} model** (AIC$_C$ and effect sizes of models without influential data point in brackets)

Table A IV-I 5 Details on the full and null LMMs without the influential data point regarding males' changes in their rates of giving grooming after a predation event, using demonstrated reactive scope (DRS and DRS_{CV}), mean fGCM concentrations, and the dyadic CSI to the killed individual as predictors. Models included age, rank category, and predation event 1 or 2.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	ω	Marginal R^2	Cond. R^2
full model:					-35.37	4.72	0.041	20.74%	20.74%
Intercept	-0.02	0.03	-0.08, 0.04	.534					
DRS	-0.0001	0.0001	-0.0003, 0.0001	.247					
age	0.02	0.01	-0.01, 0.04	.200					
rank category	0.01	0.01	-0.02, 0.04	.616					
pred. 2	0.02	0.02	-0.02, 0.06	.286					
full model:					-36.59	3.5	0.076	26.51%	26.51%
Intercept	0.01	0.03	-0.05, 0.08	.670					
DRS_{CV}	-0.08	0.05	-0.18, 0.02	.112					
age	0.02	0.01	-0.01, 0.04	.131					
rank category	0.0004	0.01	-0.03, 0.03	.976					
pred. 2	0.02	0.02	-0.02, 0.06	.254					
full model:					-20.42	0	0.436	14.00%	14.00%
Intercept	-0.03	0.07	-0.19, 0.12	.659					
mean fGCM	0.00001	0.00004	-0.0001, 0.0001	.736					
age	0.01	0.01	-0.01, 0.03	.312					
pred. 2	0.02	0.02	-0.02, 0.07	.244					
full model:					-34.26	5.38	0.024	15.13%	15.13%
Intercept	-0.003	0.04	-0.08, 0.07	.923					
CSI	-0.03	0.05	-0.13, 0.08	.607					
age	0.01	0.01	-0.01, 0.03	.424					
rank category	0.003	0.01	-0.03, 0.03	.858					
pred. 2	0.02	0.02	-0.02, 0.06	.339					
null model:					-40.03	0.06	0.423	13.68%	13.68%
Intercept	-0.01	0.03	-0.08, 0.05	.656					
age	0.01	0.01	-0.01, 0.03	.476					
rank category	0.003	0.01	-0.03, 0.03	.814					
pred. 2	0.02	0.02	-0.02, 0.07	.247					

Table A IV-I 6 Details on the full and null LMMs regarding males' changes in their rates of receiving grooming after a predation event, using demonstrated reactive scope (DRS and DRS_{CV}), mean fGCM concentrations, and the dyadic CSI to the killed individual as predictors. Models included age, rank category, and predation event 1 or 2.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	ω	Marginal R^2	Cond. R^2
full model DRS: *****					13.62 (0.49)	5.56 (5.83)	0.028	10.42% (28.65%)	10.42%
Intercept	0.10	0.18	-0.27, 0.47	.572					
DRS	0.00001	0.0004	-0.001, 0.001	.986					
age	-0.06	0.05	-0.17, 0.05	.280					
rank category	0.02	0.06	-0.11, 0.15	.774					
pred. 2	0.01	0.08	-0.16, 0.18	.929					
full model DRS_{CV}: *****					13.53 (0.49)	5.47 (5.83)	0.029	10.89% (28.49%)	10.89%
Intercept	0.08	0.19	-0.31, 0.47	.673					
DRS_{CV}	0.06	0.20	-0.38, 0.5	.767					
age	-0.06	0.05	-0.17, 0.04	.211					
rank category	0.02	0.06	-0.10, 0.15	.730					
pred. 2	0.01	0.08	-0.16, 0.18	.937					

full model fGCM: *****					8.14 (-4.38)	0.08 (0.96)	0.431	10.01% (20.82%)	10.01%
Intercept	0.16	0.35	-0.57, 0.89	.656					
mean fGCM	-0.00001	0.0002	-0.0003, 0.0003	.924					
age	-0.05	0.04	-0.13, 0.03	.192					
pred. 2	0.01	0.08	-0.17, 0.18	.952					
full model CSI: *****					11.95 (0.13)	3.89 (5.47)	0.064	18.73% (30.60%)	18.73%
Intercept	0.17	0.18	-0.19, 0.54	.345					
CSI	-0.11	0.08	-0.27, 0.06	.203					
age	-0.05	0.04	-0.13, 0.03	.225					
rank category	0.03	0.06	-0.09, 0.14	.635					
pred. 2	-0.03	0.08	-0.20, 0.14	.731					
null model:					8.06 (-5.34)	0 (0)	0.448	10.42% (27.28%)	10.42%
Intercept	0.10	0.18	-0.26, 0.47	.572					
age	-0.06	0.04	-0.15, 0.03	.201					
rank category	0.02	0.06	-0.11, 0.14	.771					
pred. 2	0.01	0.08	-0.16, 0.18	.929					

*** nat influential point in DRS_{CV} model** (AIC_C and effect sizes of models without influential data point in brackets)

Table A IV-I 7 Details on the full and null LMMs without the influential data point regarding males' changes in their rates of receiving grooming after a predation event, using demonstrated reactive scope (DRS and DRS_{CV}), mean fGCM concentrations, and the dyadic CSI to the killed individual as predictors. Models included age, rank category, and predation event 1 or 2.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	**ω**	Marginal R^2	Cond. R^2
full model:					0.49	5.83	0.030	28.65%	31.07%
Intercept	0.07	0.08	-0.13, 0.24	.454					
DRS	-0.0001	0.0003	-0.001, 0.0005	.655					
age	0.03	0.04	-0.06, 0.11	.415					
rank category	-0.08	0.04	-0.17, 0.02	.083					
pred. 2	0.08	0.05	-0.04, 0.19	.191					
full model:					0.49	5.83	0.030	28.49%	32.04%
Intercept	0.09	0.1	-0.14, 0.29	.368					
DRS_{CV}	-0.06	0.14	-0.37, 0.24	.653					
age	0.03	0.04	-0.05, 0.11	.42					
rank category	-0.09	0.04	-0.18, 0.02	.072					
pred. 2	0.08	0.05	-0.04, 0.19	.181					
full model:					-4.38	0.96	0.345	20.82%	41.84%
Intercept	-0.34	0.26	-0.88, 0.21	.211					
mean fGCM	0.0002	0.0001	-0.0001, 0.0004	.215					
age	-0.003	0.03	-0.07, 0.06	.919					
pred. 2	0.09	0.05	-0.03, 0.2	.116					
full model:					0.13	5.47	0.036	30.60%	30.60%
Intercept	0.09	0.08	-0.11, 0.26	.316					
CSI	-0.04	0.06	-0.16, 0.08	.445					
age	0.02	0.03	-0.05, 0.09	.479					
rank category	-0.08	0.04	-0.17, 0.02	.091					
pred. 2	0.06	0.06	-0.06, 0.18	.327					
null model:					-5.34	0	0.559	27.28%	32.77%
Intercept	0.07	0.09	-0.13, 0.25	.444					
age	0.02	0.03	-0.05, 0.09	.517					
rank category	-0.08	0.04	-0.17, 0.02	.087					
pred. 2	0.08	0.05	-0.04, 0.19	.184					

Table A IV-I 8 Details on the full and null LMMs regarding males' changes in aggression rates after a predation event, using demonstrated reactive scope (DRS and DRS_{CV}), mean fGCM concentrations, and the dyadic CSI to the killed individual as predictors. Models included age, rank category, and predation event 1 or 2.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	**ω**	Marginal R^2	Cond. R^2
full model DRS:					134.92	5.46	0.028	2.77%	2.77%
Intercept	1.23	5.16	-9.44, 11.9	.814					
DRS	0.004	0.01	-0.02, 0.03	.757					
age	0.11	1.47	-2.92, 3.16	.940					
rank category	-0.49	1.70	-4.04, 3.03	.776					
pred. 2	-1.33	2.41	-6.32, 3.66	.588					
full model DRS_{CV}:					134.81	5.35	0.030	3.43%	3.43%
Intercept	0.18	5.5	-11.20, 11.56	.975					
DRS_{CV}	2.72	5.85	-9.40, 14.85	.647					
age	0.03	1.41	-2.9, 2.97	.982					
rank category	-0.27	1.72	-3.85, 3.29	.878					
pred. 2	-1.37	2.40	-6.34, 3.61	.577					
full model fGCM:					129.52	0.06	0.419	1.86%	1.86%
Intercept	-0.07	10.07	-20.91, 20.76	.994					
mean fGCM	0.0003	0.004	-0.01, 0.01	.952					
age	0.22	1.07	-2.01, 2.45	.839					
pred. 2	-1.27	2.42	-6.27, 3.74	.607					
full model CSI: **§**					132.55	3.09	0.092	15.38%	15.44%
Intercept	-1.35	5.04	-14.93, 9.54	.793					
CSI	3.74	2.29	-7.29, 19.64	.121					
age	0.19	1.15	-2.37, 2.66	.873					
rank category	-0.78	1.6	-4.34, 2.82	.637					
pred. 2	-0.03	2.39	-4.92, 5.42	.990					
null model:					129.46	0	0.432	2.21%	2.21%
Intercept	1.10	5.16	-9.56, 11.77	.833					
age	0.37	1.22	-2.16, 2.91	.767					
rank category	-0.43	1.7	-3.96, 3.08	.803					
pred. 2	-1.32	2.42	-6.33, 3.68	.591					

§ 95%-CI had to be calculated with the outlier (scf) excluded, as profiling was otherwise not possible

Table A IV-I 9 Details on the full and null LMMs regarding males' changes in agonism rates after a predation event, using demonstrated reactive scope (DRS and DRS_{CV}), mean fGCM concentrations, and the dyadic CSI to the killed individual as predictors. Models included age, rank category, and predation event 1 or 2.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	**ω**	Marginal R^2	Cond. R^2
full model DRS:					131.63	5.89	0.021	4.63%	4.63%
Intercept	-1.94	4.71	-11.67, 7.80	.686					
DRS	0.01	0.01	-0.02, 0.03	.604					
age	-1.14	1.34	-3.91, 1.67	.404					
rank category	0.49	1.56	-2.82, 3.71	.757					
pred. 2	0.72	2.20	-3.83, 5.27	.747					
full model DRS_{CV}:					131.66	5.92	0.020	4.49%	4.49%
Intercept	-3.05	5.04	-13.47, 7.38	.553					
DRS_{CV}	2.7	5.36	-8.47, 13.87	.621					
age	-1.08	1.3	-3.77, 1.63	.414					
rank category	0.74	1.58	-2.62, 4.01	.643					
pred. 2	0.68	2.20	-3.87, 5.24	.759					
full model fGCM:					126.43	0.69	0.278	2.59%	2.59%
Intercept	0.69	9.24	-18.51, 19.81	.941					
mean fGCM	-0.001	0.004	-0.01, 0.01	.814					
age	-0.59	0.99	-2.66, 1.48	.560					
pred. 2	0.63	2.22	-3.97, 5.22	.782					
full model CSI: *****					125.74 (121.16)	0 (2.25)	0.391	32.3% (27.11%)	32.3%
Intercept	-5.51	4.17	-14.14, 3.15	.204					
CSI	**5.15**	**1.9**	**1.22, 9.09**	**.014**					
age	-1	0.95	-3.03, 1.06	.308					
rank category	0.11	1.32	-2.84, 2.86	.937					
pred. 2	2.51	1.98	-1.59, 6.07	.221					

null model:					126.34 (118.91)	0.6 (0)	0.290	3.07% (7.77%)	3.07%
Intercept	-2.13	4.73	-11.91, 7.66	.658					
age	-0.75	1.12	-3.08, 1.61	.512					
rank category	0.58	1.56	-2.76, 3.81	.712					
pred. 2	0.73	2.22	-3.86, 5.31	.747					

*** scf influential point in CSI model** (AIC$_C$ and effect sizes of models without influential data point in brackets)

Table A IV-I 10 Details on the full LMM including the CSI to the killed individual and null model without the influential data point regarding males' changes in agonism rates after a predation event. Models included age, rank category, and predation event 1 or 2.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2	Cond. R^2
full model:					121.16	2.25	0.245	27.11%	27.11%
Intercept	-4.99	3.43	-12.12, 2.32	.164					
CSI	10.28	4.95	-0.08, 20.56	.053					
age	-1.17	0.95	-3.15, 0.82	.238					
rank category	0.36	1.33	-2.43, 3.13	.789					
pred. 2	2.97	2.01	-1.20, 7.14	.158					
null model:					118.91	0	0.755	7.77%	16.15%
Intercept	-0.91	3.32	-7.80, 6.76	.789					
age	-0.79	1.1	-3.20, 1.68	.493					
rank category	-0.03	1.54	-3.67, 3.18	.983					
pred. 2	1.67	2.05	-2.74, 6.07	.439					

Table A IV-I 11 Details on the full and null LMMs regarding females' changes in scratching rates after a predation event, using demonstrated reactive scope (DRS and DRS$_{CV}$), mean fGCM concentrations, and the dyadic CSI to the killed individual as predictors. Models included age, rank category, predation event 1 or 2, and the females' reproductive state at the time (with cycling as reference category).

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2	Cond. R^2
full model DRS:					333.49	1.38	0.184	15.05%	15.05%
Intercept	-9.12	15.4	-40.09, 21.89	.557					
DRS	0.01	0.01	-0.002, 0.02	.127					
age	-4.82	3.53	-11.92, 2.28	.180					
rank category	4.19	3.32	-2.48, 10.86	.214					
reprod. (lact.)	9.63	8.95	-8.43, 27.63	.289					
reprod. (preg.)	12.54	9.85	-7.27, 32.34	.211					
pred. 2	2.39	5.30	-8.29, 13.06	.655					
full model DRS$_{CV}$:					332.11	0	0.366	18.23%	18.23%
Intercept	-10.85	15.14	-41.30, 19.59	.478					
DRS$_{CV}$	11.65	5.87	-0.15, 23.45	.055					
age	-5.94	3.59	-13.15, 1.28	.106					
rank category	3.43	3.27	-3.15, 10.00	.301					
reprod. (lact.)	8.94	8.79	-8.76, 26.63	.316					
reprod. (preg.)	11.02	9.67	-8.44, 30.48	.262					
pred. 2	2.33	5.20	-8.14, 12.79	.657					
full model fGCM:					335.61	3.5	0.064	9.92%	9.92%
Intercept	5.01	32.44	-0.24, 71.17	.878					
mean fGCM	-0.005	0.01	-0.02, 0.01	.619					
age	-3.98	3.81	-11.69, 3.68	.302					
rank category	2.81	4.22	-5.76, 11.31	.510					
reprod. (lact.)	11.75	9.10	-6.94, 30.07	.205					
reprod. (preg.)	12.62	10.19	-7.88, 33.13	.223					
pred. 2	2.04	5.46	-8.93, 13.02	.710					
full model CSI:					335.76	3.65	0.059	9.54%	9.54%
Intercept	-8.67	15.96	-40.77, 23.61	.590					
CSI	0.28	0.89	-1.51, 2.07	.757					
age	-3.6	3.71	-11.05, 3.86	.338					
rank category	4.06	3.42	-2.84, 10.94	.242					
reprod. (lact.)	11.41	9.17	-7.28, 29.85	.221					
reprod. (preg.)	11.94	10.15	-8.48, 32.37	.247					
pred. 2	1.70	5.49	-9.35, 12.75	.758					

null model:					332.34	0.23	0.328	9.29%	9.29%
Intercept	-9.17	15.9	-41.16, 23.12	.567					
age	-3.2	3.48	-10.24, 3.81	.364					
rank category	4.06	3.42	-2.87, 10.94	.243					
reprod. (lact.)	11.69	9.14	-7.06, 30.07	.209					
reprod. (preg.)	12.04	10.16	-8.40, 32.48	.244					
pred. 2	1.89	5.47	-9.11, 12.89	.732					

Table A IV-I 12 Details on the full and null LMMs regarding females' changes in their rates of all self-directed behaviours after a predation event, using demonstrated reactive scope (DRS and DRS$_{CV}$), mean fGCM concentrations, and the dyadic CSI to the killed individual as predictors. Models included age, rank category, predation event 1 or 2, and the females' reproductive state at the time (with cycling as reference category).

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2	Cond. R^2
full model DRS:					337.21	1.5	0.198	17.93%	17.93%
Intercept	-12.28	16.19	-44.85, 20.28	.453					
DRS	0.01	0.01	-0.002, 0.02	.092					
age	-5.26	3.71	-12.72, 2.20	.164					
rank category	5.07	3.49	-1.94, 12.09	.154					
reprod. (lact.)	10.76	9.41	-8.19, 29.68	.260					
reprod. (preg.)	17.16	10.35	-3.67, 37.99	.106					
pred. 2	3.05	5.58	-8.17, 14.27	.588					
full model DRS$_{CV}$:					335.71	0	0.419	21.26%	21.26%
Intercept	-14.26	15.89	-46.22, 17.71	.376					
DRS$_{CV}$	**13.28**	**6.16**	**0.88, 25.66**	**.038**					
age	-6.50	3.77	-14.07, 1.07	.093					
rank category	4.2	3.43	-2.71, 11.10	.229					
reprod. (lact.)	10.02	9.23	-8.55, 28.59	.285					
reprod. (preg.)	15.42	10.15	-5.01, 35.85	.137					
pred. 2	2.97	5.46	-8.01, 13.96	.59					
full model fGCM:					339.90	4.19	0.052	11.59%	11.59%
Intercept	0.62	34.37	-68.55, 70.38	.986					
mean fGCM	-0.004	0.01	-0.03, 0.02	.668					
age	-4.1	4.03	-12.24, 4.02	.317					
rank category	3.77	4.48	-5.27, 12.78	.405					
reprod. (lact.)	13.21	9.65	-6.49, 32.62	.179					
reprod. (preg.)	17.11	10.80	-4.62, 38.84	.122					
pred. 2	2.62	5.78	-9.02, 14.25	.654					
full model CSI:					339.68	3.97	0.058	12.13%	12.13%
Intercept	-11.24	16.83	-45.09, 22.66	.508					
CSI	0.60	0.94	-1.29, 2.49	.525					
age	-4.24	3.91	-12.1, 3.62	.284					
rank category	4.93	3.60	-2.33, 12.18	.180					
reprod. (lact.)	12.54	9.67	-7.04, 31.99	.203					
reprod. (preg.)	16.37	10.70	-5.17, 37.90	.135					
pred. 2	2.07	5.79	-9.58, 13.72	.723					
null model:					336.57	0.86	0.274	11.13%	11.13%
Intercept	-12.34	16.83	-46.21, 21.66	.468					
age	-3.38	3.69	-10.81, 4.04	.365					
rank category	4.91	3.62	-2.39, 12.20	.182					
reprod. (lact.)	13.16	9.27	-6.57, 32.62	.182					
reprod. (preg.)	16.58	10.76	-5.06, 38.23	.132					
pred. 2	2.47	5.79	-9.17, 14.12	.672					

Table A IV-I 13 Details on the full and null LMMs regarding females' changes in their rates of giving grooming after a predation event, using demonstrated reactive scope (DRS and DRS$_{CV}$), mean fGCM concentrations, and the dyadic CSI to the killed individual as predictors. Models included age, rank category, predation event 1 or 2, and the females' reproductive state at the time (with cycling as reference category).

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2	Cond. R^2
full model DRS:					-22.11	2.51	0.126	15.48%	21.53%
Intercept	-0.06	0.13	-0.32, 0.21	.663					
DRS	0.0001	0.00005	-0.0001, 0.0002	.319					
age	-0.03	0.03	-0.09, 0.03	.283					
rank category	0.05	0.03	-0.01, 0.11	.077					
reprod. (lact.)	-0.02	0.07	-0.17, 0.13	.779					
reprod. (preg.)	0.005	0.08	-0.16, 0.17	.951					
pred. 2	0.002	0.04	-0.08, 0.09	.972					
full model DRS$_{CV}$:					-21.83	2.79	0.109	14.77%	22.02%
Intercept	-0.06	0.13	-0.33, 0.21	.633					
DRS$_{CV}$	0.04	0.05	-0.06, 0.15	.399					
age	-0.03	0.03	-0.1, 0.03	.285					
rank category	0.05	0.03	-0.01, 0.11	.1					
reprod. (lact.)	-0.02	0.07	-0.17, 0.13	.785					
reprod. (preg.)	-0.002	0.08	-0.17, 0.16	.980					
pred. 2	0.0004	0.04	-0.09, 0.09	.992					
full model fGCM:					-23.35	1.27	0.235	18.51%	22.05%
Intercept	-0.41	0.26	-0.94, 0.13	.130					
mean fGCM	0.0001	0.0001	-0.00004, 0.0003	.138					
age	-0.005	0.03	-0.07, 0.06	.876					
rank category	**0.08**	**0.03**	**0.01, 0.15**	**.024**					
reprod. (lact.)	-0.01	0.07	-0.16, 0.14	.89					
reprod. (preg.)	-0.01	0.08	-0.17, 0.15	.909					
pred. 2	-0.005	0.04	-0.09, 0.08	.91					
full model CSI:					-21.4	3.22	0.088	13.56%	22.94%
Intercept	-0.05	0.13	-0.32, 0.23	.718					
CSI	0.004	0.01	-0.01, 0.02	.587					
age	-0.03	0.03	-0.09, 0.03	.353					
rank category	0.05	0.03	-0.01, 0.11	.089					
reprod. (lact.)	-0.02	0.07	-0.17, 0.14	.840					
reprod. (preg.)	0.001	0.08	-0.17, 0.17	.991					
pred. 2	-0.004	0.04	-0.09, 0.08	.93					
null model:					-24.62	0	0.422	12.88%	21.83%
Intercept	-0.06	0.13	-0.32, 0.22	.68					
age	-0.02	0.03	-0.08, 0.04	.425					
rank category	0.05	0.03	-0.01, 0.11	.090					
reprod. (lact.)	-0.01	0.07	-0.17, 0.14	.879					
reprod. (preg.)	0.0005	0.08	-0.17, 0.17	.996					
pred. 2	-0.001	0.04	-0.09, 0.09	.978					

Table A IV-I 14 Details on the full and null LMMs regarding females' changes in their rates of receiving grooming after a predation event, using demonstrated reactive scope (DRS and DRS$_{CV}$), mean fGCM concentrations, and the dyadic CSI to the killed individual as predictors. Models included age, rank category, predation event 1 or 2, and the females' reproductive state at the time (with cycling as reference category).

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2	Cond. R^2
full model DRS:					17.52	3.36	0.098	9.24%	16.87%
Intercept	-0.02	0.22	-0.47, 0.43	.936					
DRS	-0.00003	0.0001	-0.0002, 0.0001	.690					
age	0.08	0.05	-0.02, 0.19	.132					
rank category	-0.01	0.05	-0.11, 0.09	.831					
reprod. (lact.)	-0.09	0.13	-0.35, 0.17	.472					
reprod. (preg.)	-0.16	0.14	-0.44, 0.12	.253					
pred. 2	-0.02	0.07	-0.17, 0.12	.753					

full model DRS$_{CV}$:					17.53	3.37	0.097	9.23%	16.53%
Intercept	-0.02	0.22	-0.48, 0.42	.917					
DRS$_{CV}$	0.03	0.09	-0.15, 0.21	.699					
age	0.07	0.05	-0.04, 0.18	.225					
rank category	-0.01	0.04	-0.11, 0.09	.811					
reprod. (lact.)	-0.11	0.13	-0.36, 0.15	.403					
reprod. (preg.)	-0.16	0.14	-0.44, 0.12	.249					
pred. 2	-0.02	0.07	-0.17, 0.13	.785					
full model fGCM:					17.67	3.51	0.091	8.85%	16.67%
Intercept	0.03	0.46	-0.92, 0.97	.951					
mean fGCM	-0.00002	0.0001	-0.0003, 0.0003	.909					
age	0.07	0.05	-0.04, 0.18	.198					
rank category	-0.01	0.06	-0.14, 0.11	.818					
reprod. (lact.)	-0.1	0.13	-0.35, 0.16	.435					
reprod. (preg.)	-0.16	0.14	-0.44, 0.12	.266					
pred. 2	-0.02	0.07	-0.17, 0.13	.776					
full model CSI:					16.21	2.05	0.189	12.3%	20.10%
Intercept	0.01	0.22	-0.45, 0.45	.978					
CSI	0.01	0.01	-0.01, 0.04	.229					
age	0.05	0.05	-0.05, 0.16	.303					
rank category	-0.01	0.05	-0.11, 0.09	.847					
reprod. (lact.)	-011	0.12	-0.36, 0.14	.370					
reprod. (preg.)	-0.16	0.14	-0.44, 0.11	.238					
pred. 2	-0.03	0.07	-0.17, 0.11	.667					
null model:					14.16	0	0.525	8.81%	16.69%
Intercept	-0.02	0.22	-0.47, 0.43	.935					
age	0.07	0.05	-0.03, 0.18	.147					
rank category	-0.01	0.05	-0.11, 0.09	.841					
reprod. (lact.)	-0.1	0.13	-0.35, 0.16	.435					
reprod. (preg.)	-0.16	0.14	-0.44, 0.12	.258					
pred. 2	-0.02	0.07	-0.17, 0.13	.771					

Table A IV-I 15 Details on the full and null LMMs regarding females' changes in aggression rates after a predation event, using demonstrated reactive scope (DRS and DRS$_{CV}$), mean fGCM concentrations, and the dyadic CSI to the killed individual as predictors. Models included age, rank category, predation event 1 or 2, and the females' reproductive state at the time (with cycling as reference category).

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2	Cond. R^2
full model DRS: *****					225.73 (206.61)	3.52 (2.81)	0.097	18.64% (42.83%)	22.68% (59.54%)
Intercept	-1.22	3.65	-11.57, 6.31	.742					
DRS	-0.0001	0.001	-0.003, 0.003	.964					
age	-0.25	0.84	-2.00, 1.59	.773					
rank category	-0.35	0.79	-1.94, 1.54	.670					
reprod. (lact.)	**4.61**	**2.11**	**0.10, 11.76**	**.037**					
reprod. (preg.)	4.24	2.31	-0.65, 10.79	.075					
pred. 2	-1.80	1.21	-4.26, 0.7	.161					
full model DRS$_{CV}$: *****					225.65 (206.57)	3.44 (2.77)	0.101	18.13% (42.66%)	19.94% (59.95%)
Intercept	-1.10	3.62	-11.39, 6.26	.764					
DRS$_{CV}$	0.42	1.41	-2.87, 3.29	.769					
age	-0.36	0.86	-2.14, 1.55	.683					
rank category	-0.38	0.78	-1.96, 1.51	.635					
reprod. (lact.)	**4.32**	**2.1**	**-0.02, 11.57**	**.049**					
reprod. (preg.)	4.05	2.30	-0.69, 10.68	.088					
pred. 2	-1.77	1.22	-4.24, 0.72	.171					
full model fGCM: *****					225.45 (207.44)	3.24 (3.64)	0.111	18.6% (41.76%)	20.49% (58.31%)
Intercept	2.40	7.4	-16.12, 17.29	.751					
mean fGCM	-0.001	0.002	-0.01, 0.004	.604					
age	-0.45	0.87	-2.27, 1.43	.613					
rank category	-0.66	0.96	-2.61, 1.61	.505					
reprod. (lact.)	**4.44**	**2.06**	**0.16, 11.43**	**.041**					
reprod. (preg.)	4.23	2.31	-0.52, 10.68	.076					
pred. 2	-1.75	1.22	-4.22, 0.74	.174					

*full model CSI: **					225.22 (206.45)	3.01 (2.65)	0.125	21.11% (44.75%)	28.85% (65.31%)
Intercept	-1.31	3.7	-12.32, 6.5	.728					
CSI	0.14	0.2	-0.26, 0.54	.470					
age	-0.46	0.86	-2.30, 1.36	.600					
rank category	-0.31	0.80	-1.93, 1.68	.707					
reprod. (lact.)	**4.77**	**2.09**	**0.04, 12.31**	**.030**					
reprod. (preg.)	4.48	2.3	-0.64, 11.32	.059					
pred. 2	-1.91	1.18	-4.33, 0.59	.131					
null model:					222.21 (203.80)	0 (0)	0.565	18.57% (41.69%)	22.43% (57.98%)
Intercept	-1.21	3.65	-11.51, 6.31	.744					
age	-0.26	0.80	-1.96, 1.47	.753					
rank category	-0.35	0.79	-1.94, 1.53	.67					
reprod. (lact.)	**4.57**	**2.08**	**0.14, 11.61**	**.037**					
reprod. (preg.)	4.23	2.31	-0.65, 10.74	.075					
pred. 2	-1.8	1.21	-4.26, 0.7	.161					

*** gru influential point** (AIC$_C$ and effect sizes of models without influential data point in brackets)

Table A IV-I 16 Details on the full and null LMMs without the influential data point regarding females' changes in aggression rates after a predation event, using demonstrated reactive scope (DRS and DRS$_{CV}$), mean fGCM concentrations, and the dyadic CSI to the killed individual as predictors. Models included age, rank category, and predation event 1 or 2, and the females' reproductive state at the time (with cycling as reference category).

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	ω	Marginal R^2	Cond. R^2
full model:					206.61	2.81	0.128	42.83%	59.54%
Intercept	-7.18	3.7	-15.2, 0.52	.062					
DRS	-0.001	0.001	-0.004, 0.002	.365					
age	0.81	0.88	-0.97, 2.73	.372					
rank category	-1.11	0.83	-2.87, 0.60	.200					
reprod. (lact.)	**11.59**	**2.43**	**5.63, 16.87**	**<.0001**					
reprod. (preg.)	**10.28**	**2.45**	**4.60, 15.36**	**.0003**					
pred. 2	**-2.31**	**0.98**	**-4.30, -0.17**	**.032**					
full model:					206.57	2.77	0.130	42.66%	59.95%
Intercept	-7.12	3.7	-15.007, 0.52	.064					
DRS$_{CV}$	-1.43	1.50	-4.71, 1.59	.353					
age	0.95	0.94	-0.94, 2.99	.326					
rank category	-1.04	0.83	-2.78, 0.68	.228					
reprod. (lact.)	**11.81**	**2.47**	**5.74, 17.10**	**<.0001**					
reprod. (preg.)	**10.59**	**2.49**	**4.84, 15.7**	**.0002**					
pred. 2	**-2.30**	**0.98**	**-4.28, -0.18**	**.031**					
full model:					207.44	3.64	0.084	41.76%	58.31%
Intercept	-7.94	7.90	-25.76, 8.04	.328					
mean fGCM	0.0003	0.002	-0.004, 0.01	.888					
age	0.59	0.93	-1.29, 2.65	.535					
rank category	-0.95	0.99	-3.01, 1.63	.353					
reprod. (lact.)	**11.05**	**2.41**	**5.02, 16.43**	**<.0001**					
reprod. (preg.)	**10.02**	**2.47**	**4.22, 15.19**	**.0004**					
pred. 2	**-2.25**	**1**	**-4.27, -0.06**	**.039**					
full model:					206.45	2.65	0.138	44.75%	65.31%
Intercept	-7.16	3.75	-15.47, 0.75	.066					
CSI	0.17	0.16	-0.18, 0.49	.295					
age	0.33	0.89	-1.49, 2.24	.716					
rank category	-1.03	0.86	-2.84, 0.77	.253					
reprod. (lact.)	**11.40**	**2.32**	**5.35, 16.58**	**<.0001**					
reprod. (preg.)	**10.36**	**1027**	**4.60, 15.33**	**.0002**					
pred. 2	**-2.42**	**0.95**	**-4.33, -0.3**	**.022**					
null model:					203.80	0	0.520	41.69%	57.98%
Intercept	-6.91	3.73	-15.16, 0.93	.074					
age	0.53	0.84	-1.17, 2.36	.535					
rank category	-1.03	0.83	-2.78, 0.69	.233					
reprod. (lact.)	**10.98**	**2.4**	**5.04, 16.35**	**<.0001**					
reprod. (preg.)	**9.99**	**2.47**	**4.2, 15.17**	**.0004**					
pred. 2	**-2.24**	**1**	**-4.26, -0.05**	**.040**					

Table A IV-I 17 Details on the full and null LMMs regarding females' changes in agonism rates after a predation event, using demonstrated reactive scope (DRS and DRS$_{CV}$), mean fGCM concentrations, and the dyadic CSI to the killed individual as predictors. Models included age, rank category, predation event 1 or 2, and the females' reproductive state at the time (with cycling as reference category).

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2	Cond. R^2
full model DRS: *****					279.15	3.52	0.100	12.89%	12.89%
Intercept	5.24	739	-9.71, 20.10	.483	(238.9)	(2.1)		(27.71%)	(36.88%)
DRS	-0.0001	0.003	-0.01, 0.01	.971					
age	-2.46	1.69	-5.87, 0.94	.154					
rank category	-0.19	1.59	-3.39, 3.01	.906					
reprod. (lact.)	3.97	4.29	-4.67, 12.87	.361					
reprod. (preg.)	4.67	4.72	-4.83, 14.3	.329					
pred. 2	-3.39	2.54	-8.51, 1.73	.191					
full model DRS$_{CV}$: *****					279.04	3.41	0.106	13.16%	13.16%
Intercept	5.10	7.39	-9.82, 19.97	.494	(236.8)	(0)		(32.14%)	(37.12%)
DRS$_{CV}$	0.96	2.86	-4.8, 6.73	.739					
age	-2.71	1.75	-6.23, 0.81	.130					
rank category	-0.24	1.6	-3.45, 2.97	.882					
reprod. (lact.)	3.72	4.26	-4.92, 12.59	.392					
reprod. (preg.)	4.59	4.72	-4.91, 14.19	.337					
pred. 2	-3.35	2.54	-8.46, 1.76	.195					
full model fGCM: *****					279.15	3.52	0.100	12.89%	12.89%
Intercept	5.26	10.51	-25.14, 35.69	.730	(237.68)	(0.88)		(30.26%)	(36.47%)
mean fGCM	-0.00001	0.005	-0.01, 0.01	.999					
age	-2.48	1.78	-6.06, 1.09	.170					
rank category	-0.19	1.97	-4.15, 3.77	.924					
reprod. (lact.)	3.94	4.25	-4.6, 12.75	.359					
reprod. (preg.)	4.68	4.75	-4.88, 14.36	.331					
pred. 2	3.39	2.54	-8.51, 1.73	.191					
full model CSI: *****					278.92	3.29	0.112	13.45%	13.45%
Intercept	4.88	7.40	-10.03, 19.77	.514	(240.50)	(2.82)		(24.28%)	(34.73%)
CSI	-0.2	0.41	-1.03, 0.63	.632					
age	-2.2	1.72	-5.65, 1.26	.209					
rank category	-0.19	1.59	-3.38, 3	.904					
reprod. (lact.)	4.15	4.25	-4.41, 12.82	.336					
reprod. (preg.)	4.75	4.71	-4.73, 14.28	.320					
pred. 2	-3.25	2.55	-8.38, 1.87	.209					
null model:					275.63	0	0.582	12.89%	12.89%
Intercept	5.24	7.39	-9.71, 20.10	.483	(236.91)	(0.11)		(24.28%)	(34.7%)
age	-2.48	1.62	-5.74, 0.77	.134					
rank category	-0.19	1.59	-3.39, 3.01	.907					
reprod. (lact.)	3.94	4.25	-4.6, 12.75	.359					
reprod. (preg.)	4.68	4.72	-4.82. 14.30	.328					
pred. 2	-3.39	2.54	-8.5, 1.72	.190					

*** sil influential point** (AIC$_C$ and effect sizes of models without influential data point in brackets)

Table A IV-I 18 Details on the full and null LMMs without the influential data point regarding females' changes in agonism rates after a predation event, using demonstrated reactive scope (DRS and DRS$_{CV}$), mean fGCM concentrations, and the dyadic CSI to the killed individual as predictors. Models included age, rank category, and predation event 1 or 2, and the females' reproductive state at the time (with cycling as reference category).

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2	Cond. R^2
full model:					238.9	2.1	0.113	27.71%	36.88%
Intercept	2.02	4.84	-7.75, 12.06	.68					
DRS	0.002	0.001	-0.001, 0.01	.217					
age	**-3.26**	**1.13**	**-5.64, -0.96**	**.01**					
rank category	0.66	1.06	-1.54, 2.85	.544					
reprod. (lact.)	1.99	2.79	-4.02, 7.62	.480					
reprod. (preg.)	5.94	2.99	-0.10, 11.97	.055					
pred. 2	-0.59	1.55	-3.87, 2.54	.708					

full model:					236.8	0	0.323	32.14%	37.12%
Intercept	1.36	4.63	-8.01, 10.93	.771					
DRS$_{CV}$	3.67	1.84	-0.08, 7.62	.063					
age	**-3.69**	**1.11**	**-6.05, -1.43**	**.004**					
rank category	0.44	1.01	-1.66, 2.51	.671					
reprod. (lact.)	1.75	2.68	-3.97, 7.14	.518					
reprod. (preg.)	5.54	2.9	-0.30, 11.38	.064					
pred. 2	-0.58	1.54	-3.79, 2.53	.712					
full model:					237.68	0.88	0.208	30.26%	36.47%
Intercept	16.97	9.84	-2.98, 38.13	.102					
mean fGCM	-0.01	0.003	-0.01, 0.001	.101					
age	**-3.66**	**1.15**	**-6.08, -1.32**	**.005**					
rank category	-0.69	1.27	-3.38, 1.9	.593					
reprod. (lact.)	2.6	2.68	-3.2, 8.01	.34					
reprod. (preg.)	**6.43**	**2.95**	**0.46, 12.37**	**.036**					
pred. 2	-0.54	1.55	-3.78, 2.60	.732					
full model:					240.50	3.7	0.051	24.28%	34.73%
Intercept	2.11	4.98	-7.94, 12.47	.675					
CSI	0.003	0.26	-0.54, 0.52	.992					
age	**-2.84**	**1.17**	**-5.3, -0.47**	**.025**					
rank category	0.6	1.09	-1.67. 2.85	.591					
reprod. (lact.)	2.56	2.83	-3.52, 8.27	.373					
reprod. (preg.)	5.86	3.06	-0.31, 12.03	.064					
pred. 2	-0.78	1.58	-4.12, 2.41	.626					
null model:					236.91	0.11	0.305	24.28%	34.7%
Intercept	2.10	4.96	-7.92, 12.41	.675					
age	**-2.83**	**1.11**	**-5.16, -0.56**	**.020**					
rank category	0.6	1.09	-1.67, 2.84	.591					
reprod. (lact.)	2.57	2.82	-3.48, 8.25	.370					
reprod. (preg.)	5.86	3.06	-0.31, 12.03	.064					
pred. 2	-0.78	1.57	-4.11, 2.39	.625					

BAITING

Table A IV-I 19 Details on the full and null LMs regarding males' changes in scratching rates during a baiting period compared to baseline levels, using demonstrated reactive scope (DRS and DRS$_{CV}$) and mean fGCM concentrations as predictors. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2
full model DRS:					91.49	3.35	0.147	62.58%
Intercept	33.55	6.56	18.05, 49.06	.001				
DRS	-0.03	0.02	-0.08, 0.01	.124				
age	2.05	2.53	-3.93, 8.03	.444				
rank category	**-7.86**	**3.09**	**-15.17, -0.54**	**.039**				
full model DRS$_{CV}$:					94.06	5.92	0.042	54.09%
Intercept	38.13	7.73	19.85, 56.41	.002				
DRS$_{CV}$	-8.41	8.57	-28.67, 11.85	.359				
age	0.77	2.65	-5.49, 7.03	.78				
rank category	**-9.18**	**3.31**	**-17.01, -1.34**	**.028**				
full model fGCM:					94.49	6.35	0.033	52.51%
Intercept	17.16	23.83	-36.19, 73.51	.495				
mean fGCM	0.01	0.01	-0.02, 0.03	.444				
age	0.30	2.64	-5.95, 6.56	.912				
rank category	-8.34	3.73	-17.15, 0.47	.060				
null model:					88.14	0	0.780	52.07%
Intercept	35.53	7.24	18.82, 52.23	.001				
age	0.24	2.59	-5.73, 6.20	.929				
rank category	**-9.68**	**3.27**	**-17.22, -2.15**	**.018**				

Table A IV-I 20 Details on the full and null LMs regarding males' changes in their rates of all self-directed behaviour during a baiting period compared to baseline levels, using demonstrated reactive scope (DRS and DRS$_{CV}$) and mean fGCM concentrations as predictors. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2
full model DRS:					101.12	6.14	0.041	53.37%
Intercept	38.73	10.16	14.72, 62.75	.007				
DRS	-0.03	0.03	-0.1, 0.04	.399				
age	3.56	3.92	-5.70, 12.82	.394				
rank category	**-12.62**	**4.79**	**-23.95, -1.28**	**.034**				
full model DRS$_{CV}$:					102.08	7.1	0.026	49.75%
Intercept	41.79	11.13	15.48, 68.11	.007				
DRS$_{CV}$	-4.82	12.33	-33.98, 24.35	.708				
age	2.42	3.81	-6.59, 11.43	.546				
rank category	**-13.78**	**4.77**	**-25.06, -2.5**	**.023**				
full model fGCM:					101.09	6.11	0.042	53.46%
Intercept	12.56	32.17	-63.51, 88.63	.708				
mean fGCM	0.01	0.01	-0.02, 0.04	.394				
age	2.22	3.57	-6.23, 10.66	.554				
rank category	**-12.04**	**5.03**	**-23.94, -0.14**	**.048**				
null model:					94.98	0	0.891	52.16%
Intercept	40.30	9.88	17.51, 63.09	.004				
age	2.12	3.53	-6.02, 10.25	.565				
rank category	**-14.07**	**4.46**	**-24.35, -3.79**	**.013**				

Table A IV-I 21 Details on the full and null LMs regarding males' changes in their rates of giving grooming during a baiting period compared to baseline levels, using demonstrated reactive scope (DRS and DRS$_{CV}$) and mean fGCM concentrations as predictors. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2
full model DRS:					-28.17	5.46	0.054	54.04%
Intercept	0.01	0.03	-0.06, 0.07	.838				
DRS	0.0001	0.0001	-0.0001, 0.0003	.292				
age	**-0.03**	**0.01**	**-0.06, -0.01**	**.024**				
rank category	0.03	0.01	-0.001, 0.06	.053				
full model DRS$_{CV}$:					-29.28	4.35	0.094	57.90%
Intercept	-0.01	0.03	-0.08, 0.05	.639				
DRS$_{CV}$	0.05	0.03	-0.03, 0.12	.183				
age	**-0.03**	**0.01**	**-0.05, -0.01**	**.02**				
rank category	**0.03**	**0.01**	**0.005, 0.06**	**.028**				
full model fGCM:					-26.32	7.31	0.021	46.96%
Intercept	-0.01	0.1	-0.24, 0.22	.923				
mean fGCM	0.000005	0.00004	-0.0001, 0.0001	.915				
age	**-0.03**	**0.01**	**-0.05, -0.001**	**.047**				
rank category	**0.04**	**0.02**	**0.001, 0.07**	**.046**				
null model:					-33.63	0	0.830	50.21%
Intercept	0.0005	0.03	-0.07, 0.07	.988				
age	**-0.03**	**0.01**	**-0.05, -0.003**	**.032**				
rank category	**0.04**	**0.01**	**0.01, 0.07**	**.022**				

Table A IV-I 22 Details on the full and null LMs regarding males' changes in their rates of receiving grooming during a baiting period compared to baseline levels, using demonstrated reactive scope (DRS and DRS$_{CV}$) and mean fGCM concentrations as predictors. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2
full model DRS:					-6.20	7.29	0.024	49.55%
Intercept	0.1	0.08	-0.09, 0.28	.254				
DRS	0.00004	0.0002	-0.001, 0.001	.872				
age	0.06	0.03	-0.01, 0.13	.098				
rank category	**-0.11**	**0.04**	**-0.19, -0.02**	**.024**				
full model DRS$_{CV}$:					-6.45	7.04	0.027	50.52%
Intercept	0.08	0.08	-0.11, 0.27	.342				
DRS$_{CV}$	0.04	0.09	-0.17, 0.25	.676				
age	0.06	0.03	-0.01, 0.12	.079				
rank category	**-0.11**	**0.03**	**-0.19, -0.02**	**.018**				

full model fGCM:					-6.7	6.79	0.031	51.44%
Intercept	0.04	0.24	-0.61, 0.53	.868				
mean fGCM	0.0001	0.0001	-0.0002, 0.0003	.572				
age	0.06	0.03	-0.004, 0.12	.061				
rank category	**-0.09**	**0.04**	**-0.18, -0.005**	**.042**				
null model:					-13.49	0	0.918	52.71%
Intercept	0.09	0.07	-0.07, 0.26	.226				
age	**0.06**	**0.03**	**0.0001, 0.12**	**.0497**				
rank category	**-0.10**	**0.03**	**-0.18, -0.03**	**.013**				

Table A IV-I 23 Details on the full and null LMs regarding males' changes in aggression rates during a baiting period compared to baseline levels, using demonstrated reactive scope (DRS and DRS_{CV}) and mean fGCM concentrations as predictors. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	ω	Marginal R^2
full model DRS:					98.88	7.33	0.023	0.05%
Intercept	2.43	9.18	-19.27, 24.13	.799				
DRS	-0.001	0.03	-0.07, 0.06	.981				
age	0.003	3.54	-8.37, 8.37	.999				
rank category	0.3	4.33	-9.94, 10.54	.947				
full model DRS_{CV}:					98.73	7.18	0.025	1.01%
Intercept	3.49	9.56	-19.11, 26.1	.726				
DRS_{CV}	-3.31	10.59	-28.36, 21.75	.764				
age	0.18	3.27	-7.57, 7.92	.958				
rank category	0.46	4.1	-9.23, 10.16	.913				
full model fGCM:					97.79	6.24	0.040	6.88%
Intercept	-20.07	27.69	-85.54, 45.39	.492				
mean fGCM	0.01	0.01	-0.02, 0.04	.420				
age	0.05	3.07	-7.22, 7.31	.988				
rank category	1.91	4.33	-8.33, 12.15	.672				
null model:					91.55	0	0.911	0.05%
Intercept	2.47	8.46	-17.03, 21.97	.778				
age	-0.03	3.02	-6.99, 6.93	.992				
rank category	0.26	3.81	-8.53, 9.06	.947				

Table A IV-I 24 Details on the full and null LMs regarding males' changes in agonism rates during a baiting period compared to baseline levels, using demonstrated reactive scope (DRS and DRS_{CV}) and mean fGCM concentrations as predictors. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	ω	Marginal R^2
full model DRS:					93.62	6.93	0.029	15.9%
Intercept	-4.11	7.23	-21.2, 12.97	.587				
DRS	0.01	0.02	-0.04, 0.06	.627				
age	1.77	2.79	-4.82, 8.35	.546				
rank category	0.56	3.41	-7.50, 8.62	.874				
full model DRS_{CV}:					93.96	7.27	0.024	13.94%
Intercept	-5.26	7.7	-23.45, 12.94	.517				
DRS_{CV}	1.65	8.53	-18.52, 21.82	.852				
age	2.24	2.64	-3.99, 8.48	.423				
rank category	1.05	3.30	-6.76, 8.85	.761				
full model fGCM:					93.75	7.06	0.027	15.16%
Intercept	-13.86	23.04	-68.36, 40.63	.566				
mean fGCM	0.004	0.01	-0.02, 0.03	.690				
age	2.38	2.56	-3.67, 8.43	.383				
rank category	1.81	3.60	-6.71, 10.33	.631				
null model:					86.69	0	0.920	15.25%
Intercept	-4.74	6.78	-20.38, 10.89	.504				
age	2.35	2.42	-3.23, 7.93	.361				
rank category	1.14	3.06	-5.91, 8.19	.718				

Table A IV-I 25 Details on the full and null LMs regarding females' changes in scratching rates during a baiting period compared to baseline levels, using demonstrated reactive scope (DRS and DRS$_{CV}$) and mean fGCM concentrations as predictors. Models included age, rank category, and females' reproductive state at the time (with cycling as reference category).

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2
full model DRS:					167.57	6.02	0.026	22.38%
Intercept	78.08	35.75	-0.59, 156.76	.052				
DRS	0.001	0.01	-0.02, 0.02	.895				
age	-7.40	6.91	-22.6, 7.8	.307				
rank category	-12.16	7.39	-28.43, 4.12	.128				
reprod. (lact.)	-30.48	18.3	-70.75, 9.79	.124				
reprod. (preg.)	-33.57	18.10	-73.42, 6.27	.091				
full model DRS$_{CV}$:					167.59	6.04	0.026	22.28%
Intercept	77.15	35.27	-0.48, 154.78	.051				
DRS$_{CV}$	0.07	10.47	-22.99, 23.12	.995				
age	-7.07	7.03	-22.54, 8.39	.336				
rank category	-12.00	7.45	-28.40, 4.4	.136				
reprod. (lact.)	-29.85	18.2	-69.90, 10.21	.129				
reprod. (preg.)	-33.22	18.51	-73.95, 7.52	.100				
full model fGCM:					162.55	1	0.413	39.8%
Intercept	-9.91	51.77	-123.86, 104.03	.852				
mean fGCM	0.03	0.02	-0.002, 0.07	.064				
age	-3.28	5.75	-15.94, 9.39	.580				
rank category	-3.72	7.4	-20.00, 12.55	.625				
reprod. (lact.)	**-34.04**	**15.14**	**-67.35, -0.72**	**.046**				
reprod. (preg.)	**-40.39**	**15.61**	**-74.74, -6.04**	**.025**				
null model:					161.55	0	0.534	23.82%
Intercept	77.13	33.57	3.98, 150.28	.040				
age	-7.05	6.14	-20.44, 6.33	.273				
rank category	-11.99	6.99	-27.23, 3.24	.112				
reprod. (lact.)	-29.82	16.9	-66.63, 6.99	.103				
reprod. (preg.)	-33.19	17.13	-70.51, 4.14	.077				

Table A IV-I 26 Details on the full and null LMs regarding females' changes in their rates of all self-directed behaviour during a baiting period compared to baseline levels, using demonstrated reactive scope (DRS and DRS$_{CV}$) and mean fGCM concentrations as predictors. Models included age, rank category, and females' reproductive state at the time (with cycling as reference category).

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2
full model DRS:					170.43	6.02	0.029	21.98%
Intercept	82.12	38.89	-3.48, 167.72	.058				
DRS	0.001	0.01	-0.02, 0.03	.911				
age	-6.96	7.51	-23.5, 9.58	.374				
rank category	-13.18	8.05	-30.89, 4.53	.13				
reprod. (lact.)	-30.94	19.91	-74.76, 12.88	.148				
reprod. (preg.)	-36.41	19.7	-79.76, 6.95	.092				
full model DRS$_{CV}$:					170.45	6.04	0.029	21.91%
Intercept	81.28	38.37	-3.16, 165.72	.058				
DRS$_{CV}$	0.11	11.39	-24.97, 25.19	.993				
age	-6.67	7.64	-23.49, 10.15	.401				
rank category	-13.05	8.11	-30.89, 4.79	.136				
reprod. (lact.)	-30.38	19.8	-73.95, 13.19	.153				
reprod. (preg.)	-36.10	20.13	-80.41, 8.21	.101				
full model fGCM:					165.51	1.1	0.344	37.79%
Intercept	-9.02	57.29	-135.12, 117.08	.878				
mean fGCM	0.03	0.02	-0.005, 0.07	.080				
age	-2.73	6.37	-16.74, 11.29	.677				
rank category	-4.46	8.18	-22.47, 13.56	.597				
reprod. (lact.)	-34.71	16.75	-71.58, 2.16	.063				
reprod. (preg.)	**-43.53**	**17.27**	**-81.54, -5.51**	**.029**				

null model:					164.41	0	0.597	23.44%
Intercept	81.24	36.52	1.67, 160.81	.046				
age	-6.64	6.68	-21.20, 7.92	.34				
rank category	-13.03	7.61	-29.60, 3.54	.112				
reprod. (lact.)	-30.33	18.38	-70.38, 9.71	.125				
reprod. (preg.)	-36.05	18.63	-76.65, 4.55	.077				

Table A IV-I 27 Details on the full and null LMs regarding females' changes in their rates of giving grooming during a baiting period compared to baseline levels, using demonstrated reactive scope (DRS and DRS$_{CV}$) and mean fGCM concentrations as predictors. Models included age, rank category, and females' reproductive state at the time (with cycling as reference category).

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	ω	Marginal R^2
full model DRS:					-16.77	5.99	0.042	45.43%
Intercept	-0.42	0.16	-0.76, -07	.024				
DRS	0.00001	0.0001	-0.0001, 0.0001	.852				
age	0.07	0.03	-0.0004, 0.13	.051				
rank category	**0.08**	**0.03**	**0.01, 0.15**	**.031**				
reprod. (lact.)	**0.19**	**0.08**	**0.01, 0.36**	**.043**				
reprod. (preg.)	0.07	0.08	-0.11, 0.25	.406				
full model DRS$_{CV}$:					-17.92	4.84	0.074	48.41%
Intercept	-0.41	0.15	-0.74, -0.07	.021				
DRS$_{CV}$	0.04	0.04	-0.06, 0.14	.389				
age	0.06	0.03	-0.01, 0.12	.079				
rank category	**0.08**	**0.03**	**0.01, 0.15**	**.0.5**				
reprod. (lact.)	**0.17**	**0.08**	**0.001, 0.34**	**.049**				
reprod. (preg.)	0.05	0.08	-0.12, 0.23	.513				
full model fGCM:					-16.95	5.81	0.046	45.90%
Intercept	-0.34	0.27	-0.92, 0.25	.236				
mean fGCM	-0.00003	0.0001	-0.0002, 0.0001	.704				
age	0.07	0.03	-0.0002, 0.13	.051				
rank category	0.07	0.04	-0.01, 0.16	.08				
reprod. (lact.)	**0.19**	**0.08**	**0.02, 0.37**	**.031**				
reprod. (preg.)	0.08	0.07	-0.1, 0.26	.351				
null model:					-22.76	0	0.838	47.45%
Intercept	-0.42	0.15	-0.74, -0.1	.015				
age	**0.07**	**0.03**	**0.01, 0.13**	**.026**				
rank category	**0.08**	**0.03**	**0.01, 0.15**	**.021**				
reprod. (lact.)	**0.19**	**0.07**	**0.03, 0.35**	**.026**				
reprod. (preg.)	0.07	0.08	-0.09, 0.24	.364				

Table A IV-I 28 Details on the full and null LMs regarding females' changes in their rates of receiving grooming during a baiting period compared to baseline levels, using demonstrated reactive scope (DRS and DRS$_{CV}$) and mean fGCM concentrations as predictors. Models included age, rank category, and females' reproductive state at the time (with cycling as reference category).

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	ω	Marginal R^2
full model DRS:					-15.88	5.7	0.048	30.25%
Intercept	-0.17	0.16	-0.53, 0.19	.320				
DRS	0.00002	0.00005	-0.0001, 0.0001	.645				
age	0.04	0.03	-0.03, 0.11	.258				
rank category	0.01	0.03	-0.07, 0.08	.826				
reprod. (lact.)	0.14	0.08	-0.04, 0.32	.115				
reprod. (preg.)	0.07	0.08	-0.11, 0.25	.426				
full model DRS$_{CV}$:					-15.93	5.65	0.049	30.41%
Intercept	-0.18	0.16	-0.53, 0.18	.295				
DRS$_{CV}$	0.02	0.05	-0.08, 0.13	.621				
age	0.04	0.03	-0.03, 0.11	.278				
rank category	0.01	0.03	-0.07, 0.08	.846				
reprod. (lact.)	0.14	0.08	-0.04, 0.32	.112				
reprod. (preg.)	0.06	0.08	-0.12, 0.25	.466				

full model fGCM:					-16.68	4.9	0.072	32.77%
Intercept	0.01	0.27	-0.59, 0.60	.975				
mean fGCM	-0.0001	0.0001	-0.0003, 0.0001	.401				
age	0.03	0.03	-0.03, 0.10	.274				
rank category	-0.01	0.04	-0.09, 0.08	.836				
reprod. (lact.)	0.16	0.08	-0.01, 0.34	.065				
reprod. (preg.)	0.09	0.08	-0.09, 0.27	.292				
null model:					-21.58	0	0.831	30.97%
Intercept	-0.18	0.15	-0.52, 0.15	.254				
age	0.04	0.03	-0.02, 0.10	.154				
rank category	0.01	0.03	-0.06, 0.08	.757				
reprod. (lact.)	0.15	0.08	-0.02, 0.32	.072				
reprod. (preg.)	0.07	0.08	-0.1, 0.25	.364				

Table A IV-I 29 Details on the full and null LMs regarding females' changes in aggression rates during a baiting period compared to baseline levels, using demonstrated reactive scope (DRS and DRS$_{CV}$) and mean fGCM concentrations as predictors. Models included age, rank category, and females' reproductive state at the time (with cycling as reference category).

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2
full model DRS:					98.37	4.46	0.084	33.41%
Intercept	7.82	4.67	-2.46, 18.10	.122				
DRS	-0.001	0.001	-0.004, 0.002	.322				
age	-0.68	0.90	-2.67, 1.30	.464				
rank category	-2.06	0.97	-4.19, 0.07	.057				
reprod. (lact.)	-0.18	2.39	-5.44, 5.09	.942				
reprod. (preg.)	0.14	2.37	-5.07, 5.35	.954				
full model DRS$_{CV}$:					98.21	4.3	0.091	33.9%
Intercept	8.24	4.58	-1.95, 18.33	.1				
DRS$_{CV}$	-1.48	1.36	-4.48, 1.51	.299				
age	-0.63	0.91	-2.64, 1.38	.507				
rank category	-2.01	0.97	-4.14, 0.12	.062				
reprod. (lact.)	-0.21	2.36	-5.41. 5	.931				
reprod. (preg.)	0.43	2.41	-4.87, 5.72	.863				
full model fGCM:					99.51	5.6	0.047	29.80%
Intercept	12.43	8.22	-5.67, 30.53	.159				
mean fGCM	-0.001	0.002	-0.01, 0.004	.598				
age	-1.19	0.91	-3.20, 0.82	.22				
rank category	-2.57	1.17	-5.15, 0.02	.051				
reprod. (lact.)	-0.66	2.40	-5.96, 4.63	.788				
reprod. (preg.)	0.06	2.48	-5.4, 5.51	.982				
null model:					93.91	0	0.778	30.15%
Intercept	8.78	4.59	-1.22, 18.79	.080				
age	-1.03	0.84	-2.86, 0.8	.243				
rank category	**-2.22**	**0.96**	**-4.31, -0.14**	**.039**				
reprod. (lact.)	-0.84	2.31	-5.88, 4.2	.723				
reprod. (preg.)	-0.25	2.34	-5.35, 4.86	.918				

Table A IV-I 30 Details on the full and null LMs regarding females' changes in agonism rates during a baiting period compared to baseline levels, using demonstrated reactive scope (DRS and DRS_{CV}) and mean fGCM concentrations as predictors. Models included age, rank category, and females' reproductive state at the time (with cycling as reference category).

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	**ω**	Marginal R^2
full model DRS:					124.37	6.04	0.040	30.08%
Intercept	3.96	10.03	-18.12, 26.05	.700				
DRS	0.0001	0.003	-0.01, 0.01	.988				
age	-2.26	1.94	-6.52, 2.01	.269				
rank category	-1.13	2.08	-5.70, 3.44	.596				
reprod. (lact.)	7.40	5.14	-3.90, 18.71	.177				
reprod. (preg.)	7.65	5.08	-3.53, 18.36	.160				
full model DRS_{CV}:					122.65	4.32	0.095	35.46%
Intercept	2.84	9.40	-17.86, 23.53	.769				
DRS_{CV}	-3.02	2.79	-9.17, 3.12	.302				
age	-1.42	1.87	-5.54, 2.70	.464				
rank category	-0.7	1.99	-5.07, 3.67	.732				
reprod. (lact.)	8.71	4.85	-1.97, 19.39	.100				
reprod. (preg.)	9.03	4.93	-1.83, 19.89	.095				
full model fGCM:					124.18	5.85	0.044	30.70%
Intercept	-1.01	16.99	-38.4, 36.38	.954				
mean fGCM	0.002	0.01	-0.01, 0.01	.729				
age	-2.03	1.89	-6.19, 2.12	.305				
rank category	-0.66	2.43	-6, 4.68	.791				
reprod. (lact.)	7.19	4.97	-3.75, 18.12	.176				
reprod. (preg.)	7.25	5.12	-4.02, 18.53	.184				
null model:					118.33	0	0.821	31.94%
Intercept	3.93	9.42	-16.59, 24.45	.684				
age	-2.25	1.72	-6.00, 1.51	.217				
rank category	-1.13	1.96	-5.4, 3.15	.576				
reprod. (lact.)	7.43	4.74	-2.9, 17.75	.143				
reprod. (preg.)	7.66	4.81	-2.81, 18.13	.137				

Appendix IV – II Long-term coping behaviour

Table A IV-II 1 Details on the full and null LMs regarding males' demonstrated reactive scope measured as DRS, using overall behavioural rates (i.e. scratching, all self-directed behaviour, giving grooming, receiving grooming, aggression, and agonism) as predictors. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	**ω**	Marginal R^2
full scratching:					156.25	7.11	0.017	31.06%
Intercept	-188.34	364.80	-1050.96, 674.28	.622				
scratching/hour	4.97	13.02	-25.82, 35.76	.714				
age	59.43	47.27	-52.34, 171.2	.249				
rank category	50.1	55.83	-81.92, 182.12	.399				
full SDB:					156.47	7.33	0.015	29.93%
Intercept	-64.94	314.39	-808.35, 678.46	.842				
SDB/hour	0.27	9.96	-23.28, 23.82	.979				
age	53.15	48.31	-61.08, 167.38	.308				
rank category	52.46	59.99	-89.4, 194.31	.411				
full giv. grooming:					150.42	1.28	0.305	25.76%
Intercept	23.45	107.18	-223.70, 270.59	.832				
giv. gr./hour	-743.17	3707.09	-9291.74, 7805.41	.846				
age	72.59	39.00	-17.34, 162.51	.1				
full rec. grooming:					156.47	7.33	0.015	29.92%
Intercept	-57.19	140.95	-390.49, 276.11	.697				
rec. gr./hour	0.59	1312.85	-3103.81, 3104.99	1.000				
age	52.62	44.39	-52.34, 157.59	.275				
rank category	53.04	55.92	-79.19, 185.27	.374				

full aggression:					155.11	5.97	0.029	36.53%
Intercept	114.59	213.40	-390.01, 619.19	.608				
aggression/hour	-23.38	24.34	-80.93, 34.17	.369				
age	41.55	43.15	-60.48, 143.58	.368				
rank category	39.27	54.44	-89.45, 168	.494				
full agonism:					154.38	5.24	0.042	39.98%
Intercept	207.38	245.86	-373.99, 788.75	.427				
agonism/hour	-33.45	27.63	-98.8, 31.89	.265				
age	43.56	40.91	-53.19, 140.31	.322				
rank category	36.76	52.55	-87.51, 161.03	.507				
null model:					149.14	0	0.578	32.80%
Intercept	-57.16	115.90	-324.42, 210.09	.635				
age	52.62	41.38	-42.79, 148.04	.239				
rank category	53.04	52.26	-67.47, 173.56	.340				

Table A IV-II 2 Details on the full and null LMs regarding males' demonstrated reactive scope measured as DRS_{CV}, using overall behavioural rates (i.e. scratching, all self-directed behaviour, giving grooming, receiving grooming, aggression, and agonism) as predictors. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	**ω**	Marginal R^2
full scratching:					25.28	7.4	0.012	8.79%
Intercept	0.56	0.95	-1.68, 2.8	.576				
scratching/hour	-0.01	0.03	-0.09, 0.07	.791				
age	0.05	0.12	-0.24, 0.34	.695				
rank category	0.07	0.15	-0.28, 0.41	.664				
full SDB:					25.10	7.22	0.013	9.85%
Intercept	0.63	0.80	-1.26, 2.53	.456				
SDB/hour	-0.01	0.03	-0.07, 0.05	.675				
age	0.04	0.12	-0.25, 0.33	.747				
rank category	0.08	0.15	-0.28, 0.45	.597				
full giv. grooming:					17.88	0	0.473	10.34%
Intercept	0.45	0.26	-0.14, 1.05	.118				
giv. gr./hour	-5.2	8.97	-25.88, 15.48	.578				
age	0.09	0.09	-0.13, 0.31	.373				
full rec. grooming:					25.39	7.51	0.011	8.1%
Intercept	0.3	0.36	-0.56, 1.16	.438				
rec. gr./hour	0.2	3.39	-7.83, 8.22	.955				
age	0.06	0.11	-0.21, 0.33	.603				
rank category	0.06	0.14	-0.28, 0.40	.691				
full aggression:					23.94	6.06	0.023	16.66%
Intercept	0.77	0.55	-0.53, 2.07	.204				
aggression/hour	-0.06	0.06	-0.21, 0.09	.351				
age	0.03	0.11	-0.23, 0.3	.772				
rank category	0.02	0.14	-0.31, 0.35	.872				
full agonism:					22.94	5.06	0.038	22.17%
Intercept	1.05	0.63	-0.43, 2.52	.138				
agonism/hour	-0.09	0.07	-0.26, 0.07	.227				
age	0.04	0.10	-0.21, 0.28	.727				
rank category	0.01	0.13	-0.30, 0.33	.914				
null model:					18.07	0.19	0.431	9.11%
Intercept	0.31	0.3	-0.37, 1.00	.331				
age	0.06	0.11	-0.18, 0.31	.572				
rank category	0.06	0.14	-0.25, 0.37	.667				

Table A IV-II 3 Details on the full and null LMs regarding males' mean fGCM concentrations, using overall behavioural rates (i.e. scratching, all self-directed behaviour, giving grooming, receiving grooming, aggression, and agonism) as predictors. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	**ω**	Marginal R^2
full scratching:					173.63	6.39	0.023	23.99%
Intercept	2880.88	803.89	979.99, 4781.77	.009				
scratching/hour	-22.67	28.70	-90.52, 45.18	.455				
age	-39.21	104.16	-285.51, 207.09	.718				
rank category	-153.53	123.03	-444.44, 137.41	.252				

full SDB:					173.50	6.26	0.024	24.67%
Intercept	2811.97	681.74	1199.91, 4424.03	.004				
SDB/hour	-18.24	21.60	-69.31, 32.83	.426				
age	-43.76	104.76	-291.47, 203.95	.689				
rank category	-126.91	130.09	-434.52, 180.69	.362				
full giv. grooming:					168.41	1.17	0.312	13.61%
Intercept	2156.39	242.84	1596.41, 2716.38	<.0001				
giv. gr./hour	-8222.31	8399.48	-27591.55, 11146.93	.356				
age	-62.99	88.36	-266.74, 140.76	.496				
full rec. grooming:					174.08	6.84	0.018	21.55%
Intercept	2366.96	313.82	1624.90, 3109.01	.0001				
rec. gr./hour	-1644.66	2922.91	-8556.24, 5266.92	.591				
age	-3.53	98.83	-237.23, 230.16	.972				
rank category	-163.95	124.50	-458.35, 130.45	.229				
full aggression:					172.87	5.63	0.034	27.95%
Intercept	1849.76	478.41	718.49, 2981.03	.006				
aggression/hour	58.94	54.56	-70.09, 187.96	.316				
age	19.73	96.74	-209.01, 248.48	.844				
rank category	-123.23	122.04	-420.82, 156.36	.315				
full agonism:					173.3	6.06	0.027	25.75%
Intercept	1804.30	580.82	430.89, 3177.71	.017				
agonism/hour	60.50	65.28	-93.86, 214.87	.385				
age	8.2	96.66	-220.36, 236.75	.935				
rank category	-137.50	124.15	-431.08, 156.07	.305				
null model:					167.24	0	0.562	20.99%
Intercept	2282.76	263.80	1674.44, 2891.09	<.0001				
age	-8.19	94.18	-225.38, 209	.933				
rank category	-166.95	118.96	-441.26, 107.37	.198				

Table A IV-II 4 Details on the full and null LMs regarding females' demonstrated reactive scope measured as DRS, using overall behavioural rates (i.e. scratching, all self-directed behaviour, giving grooming, receiving grooming, aggression, and agonism) as predictors. Models included age and rank category. DRS values were log$_2$-transformed to comply with model assumptions.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	ω	Marginal R^2
full scratching:					74.63	3.14	0.071	7.96%
Intercept	9.23	1.70	5.59, 12.86	<.0001				
scratching/hour	-0.06	0.05	-0.16, 0.04	.239				
age	0.05	0.39	-0.78, 0.88	.899				
rank category	0.07	0.38	-0.74, 0.89	.853				
full SDB:					74.74	3.25	0.067	7.51%
Intercept	9.26	1.75	5.54, 12.98	<.0001				
SDB/hour	-0.06	0.05	-0.15, 0.04	.254				
age	0.05	0.39	-0.78, 0.89	.896				
rank category	0.08	0.39	-0.75, 0.9	.847				
full giv. grooming:					76.38	4.89	0.029	0.57%
Intercept	7.67	1.79	3.87, 11.48	.0006				
giv. gr./hour	2.47	10.36	-19.61, 24.54	.815				
age	0.07	0.41	-0.8, 0.95	.858				
rank category	0.01	0.41	-0.86, 0.87	.988				
full rec. grooming:					75.55	4.06	0.045	4.15%
Intercept	7.48	1.47	4.35, 10.62	.0001				
rec. gr./hour	7.34	8.59	-10.96, 25.64	.406				
age	0.02	0.41	-0.85, 0.88	.967				
rank category	-0.06	0.39	-0.89, 0.77	.893				
full aggression:					71.49	0	0.340	5.75%
Intercept	8.27	0.86	6.44, 10.10	<.0001				
aggression/hour	-0.18	0.18	-0.57, 0.2	.322				
age	0.07	0.38	-0.73, 0.88	.850				
full agonism:					72.00	0.51	0.263	3.45%
Intercept	8.95	1.59	5.58, 12.32	<.0001				
agonism/hour	-0.15	0.19	-0.55, 0.26	.453				
age	-0.06	0.43	-0.97, 0.85	.891				

null model:					72.69	1.2	0.186	0.28%
Intercept	7.93	1.36	5.05, 10.82	<.0001				
age	0.08	0.4	-0.75, 0.92	.836				
rank category	-0.02	0.38	-0.83, 0.79	.965				

Table A IV-II 5 Details on the full and null LMs regarding females' demonstrated reactive scope measured as DRS$_{CV}$, using overall behavioural rates (i.e. scratching, all self-directed behaviour, giving grooming, receiving grooming, aggression, and agonism) as predictors. Models included age and rank category. DRS$_{CV}$ values were log$_2$-transformed to comply with model assumptions.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	ω	Marginal R^2
full scratching:					50.31	4.49	0.042	10.92%
Intercept	-0.45	0.9	-2.37, 1.46	.622				
scratching/hour	-0.02	0.03	-0.08, 0.03	.374				
age	0.22	0.21	-0.21, 0.66	.292				
rank category	0.1	0.20	-0.33, 0.53	.632				
full SDB:					50.56	4.74	0.037	9.92%
Intercept	-0.49	0.92	-2.46, 1.48	.602				
SDB/hour	-0.02	0.02	-0.07, 0.03	.438				
age	0.23	0.21	-0.21, 0.67	.291				
rank category	-0.1	0.20	-0.34, 0.53	.643				
full giv. grooming:					51.32	5.5	0.025	6.81%
Intercept	-1.05	0.92	-3.01, 0.92	.275				
giv. gr./hour	0.79	5.36	-10.62, 12.21	.884				
age	0.24	0.21	-0.22, 0.69	.284				
rank category	0.07	0.21	-0.38, 0.52	.740				
full rec. grooming:					50.67	4.82	0.035	9.47%
Intercept	-1.17	0.76	-2.79, 0.46	.148				
rec. gr./hour	3.29	4.46	-6.22, 12.80	.472				
age	0.21	0.21	-0.24, 0.66	.340				
rank category	0.04	0.20	-0.39, 0.47	.836				
full aggression:					45.82	0	0.393	14.59%
Intercept	-0.53	0.44	-1.46, 0.40	.245				
aggression/hour	-0.12	0.09	-0.31, 0.08	.214				
age	0.22	0.19	-0.19, 0.63	.272				
full agonism:					46.32	0.5	0.306	12.55%
Intercept	-0.004	0.81	-1.72, 1.71	.996				
agonism/hour	-0.11	0.1	-0.31, 0.1	.286				
age	0.12	0.22	-0.34, 0.58	.583				
null model:					47.59	1.77	0.162	7.11%
Intercept	-0.96	0.70	-2.45, 0.53	.190				
age	0.24	0.20	-0.2, 0.67	.261				
rank category	0.06	0.2	-0.35, 0.48	.751				

Table A IV-II 6 Details on the full and null LMs regarding females' mean fGCM concentrations, using overall behavioural rates (i.e. scratching, all self-directed behaviour, giving grooming, receiving grooming, aggression, and agonism) as predictors. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	ω	Marginal R^2
full scratching:					280.77	2.43	0.13	40.07%
Intercept	3208.99	386.86	2384.42, 4033.55	<.0001				
scratching/hour	-11.36	10.88	-34.55, 11.84	.313				
age	-153.48	88.55	-342.21, 35.25	.104				
rank category	**-245.45**	**86.92**	**-430.71, -60.19**	**.013**				
full SDB:					281.02	2.68	0.117	39.35%
Intercept	3196.95	397.93	2349.43, 4044.46	<.0001				
SDB/hour	-9.9	10.58	-32.44, 12.65	.364				
age	-152.71	89.13	-342.67, 37.26	.107				
rank category	**-246.08**	**87.72**	**-433.04, -59.11**	**.013**				
full giv. grooming:					280.65	2.31	0.141	40.41%
Intercept	3219.56	385.65	2397.57, 4041.55	<.0001				
giv. gr./hour	-2440.54	2237.45	-7209.55, 2328.47	.293				
age	-138.52	88.41	-326.96, 49.92	.138				
rank category	**-285.27**	**87.56**	**-471.91, 98.64**	**.005**				

full rec. grooming:					282.06	3.72	0.069	36.3%
Intercept	2979.79	336.93	2261.64, 3697.93	<.0001				
rec. gr./hour	-334.91	1967.72	-4529.00, 3859.18	.867				
age	-144.08	93.11	-342.55, 54.39	.143				
rank category	**-260.52**	**89.18**	**-450.60, -70.44**	**.011**				
full aggression:					281.89	3.55	0.075	25.92%
Intercept	1987.94	219.35	1522.93, 2452.94	<.0001				
aggression/hour	**103.49**	**45.91**	**6.17, 200.81**	**.039**				
age	-98.80	96.21	-302.75, 105.15	.32				
full agonism:					284.79	6.45	0.018	14.87%
Intercept	1663.00	429.83	751.79, 2574.21	.001				
agonism/hour	74.03	51.09	-34.28, 182.33	.167				
age	-32.12	115.64	-277.28, 2213.04	.785				
null model:					278.34	0	0.447	37.69%
Intercept	2959.14	304.65	2313.31, 3604.98	<.0001				
age	-147.11	88.58	-334.89, 40.47	.116				
rank category	**-262.65**	**85.58**	**-444.06, -81.24**	**.007**				

BEHAVIOUR – RANK

Table A IV-II 7 Details on the full and null LM regarding males' rates of giving grooming using rank category as predictor. Models included age.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	**ω**	Marginal R^2
full model:					-59.83	0	0.661	39.84%
Intercept	-0.001	0.01	-0.02, 0.02	.869				
rank category	**0.01**	**0.004**	**0.001, 0.02**	**.034**				
age	-0.003	0.003	-0.01, 0.004	.376				
null model:					-58.49	1.34	0.339	0.47%
Intercept	0.01	0.01	-0.01, 0.03	.202				
age	0.001	0.003	-0.01, 0.01	.833				

Table A IV-II 8 Details on the full and null LM regarding females' aggression rates using rank category as predictor. Models included age.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	**ω**	Marginal R^2
full model:					64.23	0	1	61.6%
Intercept	6.81	1.09	4.5, 9.11	<.0001				
rank category	**-0.64**	**0.31**	**-2.29, -0.99**	**<.0001**				
age	-0.33	0.32	-1, 0.34	.317				
null model:					80.55	16.32	0	0.11%
Intercept	2.09	1.04	-0.11, 4.29	.061				
age	-0.07	0.51	-1.14, 1.00	.892				

Appendix IV – III Social buffering

SOCIAL BONDS

Table IV-III 1 Details on the full and null LMs regarding males' demonstrated reactive scope measured as DRS, using measures of bond strength based on dyadic CSIs as predictors (i.e. the sum of the top 3 CSI scores, the highest CSI score, the number of strong bonds with CSI > 1, the number of weak bonds with CSI < 1). Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	ω	Marginal R^2
full sum (CSI top 3):					156.08	6.94	0.024	31.91%
Intercept	-27.87	134.68	-346.33, 290.59	.842				
sum (top 3 CSI)	-2.47	4.86	-13.95, 9.02	.627				
age	52.60	43.44	-50.13, 155.33	.265				
rank category	56.49	55.29	-74.25, 187.22	.341				
full highest CSI:					152.66	3.52	0.133	47.22%
Intercept	-5.93	108.42	-262.30, 250.44	.958				
highest CSI	-12.65	7.42	-30.20, 4.91	.132				
age	62.94	37.68	-26.16, 152.04	.139				
rank category	65.15	47.51	-47.19, 177.48	.213				
full no. strong bonds:					154.79	5.65	0.046	38.01%
Intercept	50.48	152.31	-309.68, 410.63	.750				
no. strong bonds	-18.80	17.48	-60.14, 22.54	.318				
age	55.08	41.04	-41.98, 152.13	.222				
rank category	34.83	54.46	-93.95, 163.61	.543				
full no. weak bonds:					156	6.86	0.025	32.30%
Intercept	-323.05	492.10	-1486.68, 840.59	.533				
no. weak bonds	10.30	18.48	-33.40, 54.01	.595				
age	53.52	43.31	-48.90, 155.94	.256				
rank category	43.44	57.32	-92.09, 178.98	.473				
null model:					149.14	0	0.772	32.80%
Intercept	-57.16	115.90	-324.42, 210.09	.635				
age	52.62	41.38	-42.79, 148.04	.239				
rank category	53.04	52.26	-67.47, 173.56	.340				

Table IV-III 2 Details on the full and null LMs regarding males' demonstrated reactive scope measured as DRS_CV, using measures of bond strength based on dyadic CSIs as predictors (i.e. the sum of the top 3 CSI scores, the highest CSI score, the number of strong bonds with CSI > 1, the number of weak bonds with CSI < 1). Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	ω	Marginal R^2
full sum (CSI top 3):					25.33	7.26	0.023	8.50%
Intercept	0.28	0.35	-0.56, 1.11	.458				
sum (top 3 CSI)	0.003	0.01	-0.03, 0.03	.837				
age	0.06	0.11	-0.21, 0.33	.597				
rank category	0.06	0.15	-0.29, 0.4	.709				
full highest CSI:					23.79	5.72	0.050	17.48%
Intercept	0.40	0.31	-0.33, 1.13	.238				
highest CSI	-0.02	0.02	-0.07, 0.03	.329				
age	0.08	0.11	-0.17, 0.34	.475				
rank category	0.08	0.14	-0.24, 0.40	.567				
full no. strong bonds:					25.36	7.29	0.023	8.28%
Intercept	0.35	0.42	-0.65, 1.35	.435				
no. strong bonds	-0.01	0.05	-0.12, 0.11	.886				
age	0.06	0.11	-0.21, 0.33	.593				
rank category	0.05	0.15	-0.31, 0.41	.736				
full no. weak bonds:					25.23	7.16	0.025	9.12%
Intercept	0.73	1.29	-2.32, 3.78	.590				
no. weak bonds	-0.02	0.05	-0.13, 0.1	.748				
age	0.06	0.11	-0.21, 0.33	.604				
rank category	0.08	0.15	-0.28, 0.43	.631				

null model:					18.07	0	0.879	9.11%
Intercept	0.31	0.3	-0.38, 1.00	.331				
age	0.06	0.11	-0.18, 0.31	.572				
rank category	0.06	0.14	-0.25, 0.37	.667				

Table IV-III 3 Details on the full and null LMs regarding males' mean fGCM concentrations, using measures of bond strength based on dyadic CSIs as predictors (i.e. the sum of the top 3 CSI scores, the highest CSI score, the number of strong bonds with CSI > 1, the number of weak bonds with CSI < 1). Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	ω	Marginal R^2
full sum (CSI top 3):					170.29	5.92	0.039	40.35%
Intercept	2081.73	256.91	1474.25, 2689.22	<.0001				
sum (top 3 CSI)	16.92	9.27	-4.99, 38.83	.111				
age	-8.03	82.87	-203.98, 187.93	.926				
rank category	-190.59	105.47	-439.97, 58.8	.114				
full highest CSI:					173.40	9.03	0.008	25.19%
Intercept	2214.48	278.39	1556.2, 2872.77	<.001				
highest CSI	16.86	19.06	-28.22, 61.93	.406				
age	-21.94	96.75	-250.72, 206.84	.827				
rank category	-183.08	121.98	-471.52, 105.36	.177				
full no. strong bonds:					170.83	6.46	0.029	37.89%
Intercept	1933.37	315.71	1186.82, 2679.91	.0005				
no. strong bonds	61.01	36.24	-24.98, 146.70	.136				
age	-16.15	85.08	-217.32, 185.02	.855				
rank category	-107.83	112.89	-374.77, 156.11	.371				
full no. weak bonds:					164.37	0	0.746	62.37%
Intercept	4564.84	719.92	2862.49, 6267.19	.0004				
no. weak bonds	**-88.45**	**27.04**	**-152.39, -24.50**	**.014**				
age	-15.88	63.37	-165.72, 133.96	.809				
rank category	-84.54	83.85	-282.82, 113.74	.347				
null model:					167.24	2.87	0.178	20.99%
Intercept	2282.76	263.80	1674.44, 2891.09	<.0001				
age	-8.19	94.18	-225.38, 209	.933				
rank category	-166.95	118.96	-441.26, 107.37	.198				

Table IV-III 4 Details on the full and null LMs regarding females' demonstrated reactive scope measured as DRS, using measures of bond strength based on dyadic CSIs as predictors (i.e. the sum of the top 3 CSI scores, the highest CSI score, the number of strong bonds with CSI > 1, the number of weak bonds with CSI < 1). Models included age and rank category. DRS values were $\log_2$-transformed to comply with model assumptions.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	ω	Marginal R^2
full sum (CSI top 3):					75.68	2.99	0.123	3.60%
Intercept	6.68	2.10	2.2, 11.16	.006				
sum (top 3 CSI)	0.04	0.05	-0.06, 0.14	.442				
age	0.06	0.40	-0.79, 0.92	.878				
rank category	0.16	0.45	-0.79, 1.11	.724				
full highest CSI:					76.4	3.71	0.086	0.48%
Intercept	765	1.99	3.42, 11.88	.002				
highest CSI	0.01	0.07	-0.13, 0.16	.844				
age	0.1	0.41	-0.78, 0.98	.817				
rank category	0.02	0.43	-0.91, 0.94	.965				
full no. strong bonds:					75.43	2.74	0.139	4.66%
Intercept	8.94	1.76	5.2, 12.68	.0001				
no. strong bonds	-0.15	0.17	-0.51, 0.10	.377				
age	0.18	0.41	-0.7, 1.05	.675				
rank category	-0.003	0.38	-0.82, 0.82	.993				
full no. weak bonds:					76.01	3.32	0.104	2.18%
Intercept	5.83	3.80	-2.27, 13.93	.146				
no. weak bonds	0.08	0.13	-0.20, 0.36	.561				
age	0.17	0.43	-0.74, 1.08	.698				
rank category	0.02	0.39	-0.82, 0.86	.968				

null model:					72.69	0	0.547	0.28%
Intercept	7.93	1.36	5.05, 10.82	<.0001				
age	0.08	0.4	-0.75, 0.92	.836				
rank category	-0.02	0.38	-0.83, 0.79	.965				

Table IV-III 5 Details on the full and null LMs regarding females' demonstrated reactive scope measured as DRS_{CV}, using measures of bond strength based on dyadic CSIs as predictors (i.e. the sum of the top 3 CSI scores, the highest CSI score, the number of strong bonds with CSI > 1, the number of weak bonds with CSI < 1). Models included age and rank category. DRS_{CV} values were $\log_2$-transformed to comply with model assumptions.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	**ω**	Marginal R^2
full sum (CSI top 3):					51.06	3.47	0.107	7.88%
Intercept	-1.36	1.10	-3.71, 0.98	.235				
sum (top 3 CSI)	0.01	0.02	-0.04, 0.06	.640				
age	0.23	0.21	-0.22, 0.68	.287				
rank category	0.12	0.23	-0.38, 0.62	.616				
full highest CSI:					51.27	3.68	0.096	7.01%
Intercept	-0.79	1.02	-2.97, 1.4	.455				
highest CSI	-0.01	0.03	-0.08, 0.07	.811				
age	0.23	0.21	-0.23, 0.68	.300				
rank category	0.04	0.22	-0.44, 0.52	.858				
full no. strong bonds:					51.26	3.67	0.096	7.04%
Intercept	-0.81	0.93	-2.79, 1.17	.396				
no. strong bonds	-0.02	0.09	-0.21, 0.17	.801				
age	0.25	0.22	-0.21, 0.71	.265				
rank category	0.07	0.20	-0.37, 0.5	.752				
full no. weak bonds:					51.3	3.71	0.095	6.90%
Intercept	-0.6	1.98	-4.83, 3.63	.767				
no. weak bonds	-0.01	0.07	-0.16, 0.13	.846				
age	0.22	0.22	-0.25, 0.70	.335				
rank category	0.06	0.21	-0.38, 0.5	.782				
null model:					47.59	0	0.606	7.11%
Intercept	-0.96	0.70	-2.45, 0.53	.190				
age	0.24	0.20	-0.2, 0.67	.261				
rank category	0.06	0.2	-0.35, 0.48	.751				

Table IV-III 6 Details on the full and null LMs regarding females' mean fGCM concentrations, using measures of bond strength based on dyadic CSIs as predictors (i.e. the sum of the top 3 CSI scores, the highest CSI score, the number of strong bonds with CSI > 1, the number of weak bonds with CSI < 1). Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	**ω**	Marginal R^2
full sum (CSI top 3):					274.14	0	0.707	56.43%
Intercept	3782.55	390.00	2951.28, 4613.83	<.0001				
sum (top 3 CSI)	**-24.49**	**8.77**	**-43.18, -5.8**	**.014**				
age	-133.66	74.36	-292.17, 24.84	.092				
rank category	**-379.07**	**82.94**	**-555.85, -202.30**	**.0004**				
full highest CSI:					277.02	2.88	0.168	49.91%
Intercept	3550.55	389.63	2720.08, 4381.02	<.0001				
highest CSI	**-28.41**	**13.25**	**-56.65, -0.18**	**.049**				
age	**-176.29**	**81.18**	**-349.33, -3.26**	**.046**				
rank category	**-339.09**	**85.14**	**-520.56, -157.63**	**.001**				
full no. strong bonds:					281.28	7.14	0.020	38.59%
Intercept	2757.88	395.50	1914.90, 3600.86	<.0001				
no. strong bonds	30.40	37.48	-49.49, 110.29	.430				
age	-165.58	92.39	-362.51, 31.35	.093				
rank category	**-365.35**	**86.57**	**-449.86, -80.83**	**.008**				
full no. weak bonds:					281.41	7.27	0.018	37.91%
Intercept	3498.95	848.55	1690.30, 5307.59	.0009				
no. weak bonds	-19.97	29.23	-8226, 42.32	.505				
age	-169.28	95.76	-373.39, 34.82	.097				
rank category	**-271.05**	**87.90**	**-458.4, -83.69**	**.008**				

null model:					278.34	4.2	0.087	37.69%
Intercept	2959.14	304.65	2313.31, 3604.98	<.0001				
age	-147.11	88.58	-334.89, 40.67	.116				
rank category	**-262.65**	**85.58**	**-444.06, -81.24**	**.007**				

AFFILIATION NETWORK

Table IV-III 7 Details on the full and null LMs regarding males' demonstrated reactive scope measured as DRS, using measures of affiliative network position as predictors (i.e. strength, eigenvector centrality, betweenness centrality, clustering coefficient, and reach). The network was based on dyadic CSI values. Models included age and rank category. (VIFs between clustering coefficient and age were larger than 2, so age was excluded here.)

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	**ω**	Marginal R^2
full strength:					156	29.48	0	32.29%
Intercept	-9.33	148.68	-360.90, 342.24	.952				
strength	-2.00	3.60	-10.52, 6.52	.596				
age	51.99	43.31	-50.41, 154.39	.269				
rank category	54.38	54.73	-75.03, 183.79	.354				
full eigenvector centrality:					156.47	29.95	0	29.95%
Intercept	-52.98	144.61	-394.92, 288.97	.725				
eigenvector cent.	-10.24	182.49	-441.75, 421.27	.957				
age	52.66	44.23	-51.93, 157.25	.273				
rank category	52.95	55.88	-79.18, 185.09	.375				
full betweenness centrality:					156.41	29.89	0	30.23%
Intercept	-50.35	128.31	-353.77, 253.06	.706				
betweenness	-0.94	4.75	-12.17, 10.3	.850				
age	51.69	44.37	-53.22, 156.60	.282				
rank category	54.25	56.05	-78.29, 186.78	.365				
full clustering coefficient:					126.52	0	1	32.14%
Intercept	-67.58	126.56	-377.25, 242.09	.613				
clustering coef.	227.75	158.02	-158.91, 614.42	.200				
rank category	58.38	46.92	-56.44, 173.20	.260				
full reach:					155.37	28.85	0	35.33%
Intercept	54.81	175.59	-360.39, 470.01	.764				
reach	-131.54	152.94	-493.17, 230.1	.418				
age	50.64	42.13	-48.98, 150.26	.268				
rank category	36.84	56.37	-96.47, 170.14	.534				
null model:					149.14	22.62	0	32.80%
Intercept	-57.16	115.90	-324.42, 210.09	.635				
age	52.62	41.38	-42.79, 148.04	.239				
rank category	53.04	52.26	-67.47, 173.56	.340				

Table IV-III 8 Details on the full and null LMs regarding males' demonstrated reactive scope measured as DRS_{CV}, using measures of affiliative network position as predictors (i.e. strength, eigenvector centrality, betweenness centrality, clustering coefficient, and reach). The network was based on dyadic CSI values. Models included age and rank category. (VIFs between clustering coefficient and age were larger than 2, so age was excluded here.)

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	**ω**	Marginal R^2
full strength:					25.28	7.21	0.019	8.78%
Intercept	0.25	0.39	-0.68, 1.17	.546				
strength	0.003	0.01	-0.02, 0.02	.791				
age	0.06	0.11	-0.21, 0.33	.592				
rank category	0.06	0.14	-0.28, 0.4	.696				

full eigenvector centrality:					24.42	6.35	0.029	13.91%
Intercept	0.16	0.36	-0.69, 1.01	.667				
eigenvector cent.	0.37	0.45	-0.70, 1.43	.445				
age	0.06	0.11	-0.2, 0.32	.590				
rank category	0.06	0.14	-0.26, 0.39	.660				
full betweenness centrality:					24.72	6.65	0.025	12.14%
Intercept	0.25	0.32	-0.51, 1.01	.461				
betweenness	0.01	0.01	-0.02, 0.04	.525				
age	0.07	0.11	-0.19, 0.33	.544				
rank category	0.05	0.14	-0.28, 0.38	.733				
full clustering coefficient:					20.43	2.36	0.213	3.93%
Intercept	0.37	0.35	-0.48, 1.23	.324				
clustering coef.	0.2	0.44	-0.87, 1.26	.664				
rank category	0.04	0.13	-0.27, 0.36	.757				
full reach:					25.37	7.3	0.018	8.23%
Intercept	0.36	0.48	-0.77, 1.48	.480				
reach	-0.05	0.42	-1.04, 0.93	.900				
age	0.06	0.11	-0.21, 0.33	.603				
rank category	0.05	0.15	-0.31, 0.42	.737				
null model:					18.07	0	0.696	9.11%
Intercept	0.31	0.3	-0.38, 1.00	.331				
age	0.06	0.11	-0.18, 0.31	.572				
rank category	0.06	0.14	-0.25, 0.37	.667				

Table IV-III 9 Details on the full and null LMs regarding males' mean fGCM concentrations, using measures of affiliative network position as predictors (i.e. strength, eigenvector centrality, betweenness centrality, clustering coefficient, and reach). The network was based on dyadic CSI values. Models included age and rank category. (VIFs between clustering coefficient and age were larger than 2, so age was excluded here.)

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	**ω**	Marginal R^2
full strength:					170.39	28.35	0	39.86%
Intercept	1985.19	286.04	1308.82, 2661.56	.0002				
strength	12.46	6.93	-3.93, 28.86	.115				
age	-4.24	83.31	-201.24, 192.76	.961				
rank category	-175.25	105.29	-424.22, 73.72	.14				
full eigenvector centrality:					171	28.96	0	37.12%
Intercept	2046.08	279.88	1384.27, 2707.9	.0002				
eigenvector cent.	578.84	353.19	-256.33, 1414.01	.145				
age	-10.33	85.60	-212.76, 192.09	.907				
rank category	-161.81	108.15	-417.55, 93.94	.178				
full betweenness centrality:					163.51	21.47	0	64.88%
Intercept	2116.33	177.18	1697.37, 2535.29	<.0001				
betweenness	**22.84**	**6.56**	**7.33, 38.36**	**.010**				
age	14.65	61.26	-130.22, 159.52	.818				
rank category	**-196.32**	**77.39**	**-379.32, -13.31**	**.039**				
full clustering coefficient:					142.04	0	1	30.3%
Intercept	2473.7	299.7	1740.34, 3207.01	.0002				
clustering coef.	-398.9	374.2	-1314.53, 516.77	.327				
rank category	-164.7	111.1	-436.62, 107.19	.189				
full reach:					169.87	27.83	0	42.18%
Intercept	1796.63	339.41	994.05, 2599.20	.001				
reach	571.10	295.62	-127.93, 1270.14	.096				
age	0.43	81.44	-192.15, 193	.996				
rank category	-96.59	108.97	-354.26, 161.09	.405				

null model:					167.24	25.2	0	20.99%
Intercept	2282.76	263.80	1674.44, 2891.09	<.0001				
age	-8.19	94.18	-225.38, 209	.933				
rank category	-166.95	118.96	-441.26, 107.36	.198				

Table IV-III 10 Details on the full and null LMs regarding females' demonstrated reactive scope measured as DRS, using measures of affiliative network position as predictors (i.e. strength, eigenvector centrality, betweenness centrality, clustering coefficient, and reach). The network was based on dyadic CSI values. Models included age and rank category. DRS values were log$_2$-transformed to comply with model assumptions.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	ω	Marginal R^2
full strength:					76.30	3.61	0.089	0.9%
Intercept	7.17	2.63	1.56, 12.77	.016				
strength	0.01	0.04	-9.97, 0.09	.734				
age	0.07	0.41	-0.8, 0.94	.861				
rank category	0.06	0.46	-0.92, 1.04	.890				
full eigenvector centrality:					76.44	3.75	0.083	0.28%
Intercept	7.77	2.08	3.35, 12.20	.002				
eigenvector cent.	0.1	1.56	-3.22, 3.42	.95				
age	0.08	0.41	-0.80, 0.96	.851				
rank category	-0.01	0.43	-0.92, 0.90	.988				
full betweenness centrality:					75.73	3.04	0.118	3.35%
Intercept	6.8	2.17	2.16, 11.43	.007				
betweenness	0.02	0.02	-0.03, 0.07	.46				
age	0.12	0.40	-0.74, 0.99	.764				
rank category	0.17	0.46	-0.81, 1.14	.718				
full clustering coefficient:					76.42	3.73	0.084	0.39%
Intercept	7.78	1.76	4.03, 11.53	.0005				
clustering coef.	0.42	2.73	-5.41, 6.24	.881				
age	0.06	0.43	-0.84, 0.97	.881				
rank category	-0.02	0.39	-0.86, 0.82	.962				
full reach:					76.39	3.7	0.085	0.51%
Intercept	6.99	4.41	-2.41, 16.39	.134				
reach	1.06	5.02	-9.63, 11.75	.835				
age	0.1	0.41	-0.78, 0.98	.814				
rank category	-0.03	0.4	-0.88, 0.82	.943				
null model:					72.69	0	0.541	0.28%
Intercept	7.85	1.65	4.36, 11.34	.0002				
age	0.08	0.4	-0.75, 0.92	.836				
rank category	-0.02	0.38	-0.83, 0.79	.965				

Table IV-III 11 Details on the full and null LMs regarding females' demonstrated reactive scope measured as DRS$_{CV}$, using measures of affiliative network position as predictors (i.e. strength, eigenvector centrality, betweenness centrality, clustering coefficient, and reach). The network was based on dyadic CSI values. Models included age and rank category. DRS$_{CV}$ values were log$_2$-transformed to comply with model assumptions.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	ω	Marginal R^2
full strength:					51.17	3.58	0.074	7.44%
Intercept	-1.59	1.36	-4.49, 1.30	.259				
strength	0.01	0.02	-0.03, 0.05	.711				
age	0.23	0.21	-0.22, 0.68	.288				
rank category	0.11	0.24	-0.4, 0.62	.649				
full eigenvector centrality:					51.34	3.75	0.068	6.74%
Intercept	-1.15	1.07	-3.44, 1.14	.302				
eigenvector cent.	-0.07	0.81	-1.79, 1.65	.933				
age	0.24	0.21	-0.21, 0.7	.277				
rank category	0.06	0.22	-0.41, 0.53	.802				

full betweenness centrality:					48.53	0.94	0.275	17.79%
Intercept	-2.25	1.06	-4.52, 0.01	.051				
betweenness	0.02	0.01	-0.01, 0.04	.142				
age	0.28	0.2	-0.14, 0.7	.179				
rank category	0.25	0.22	-0.23, 0.73	.284				
full clustering coefficient:					51.28	3.69	0.070	6.98%
Intercept	-1.15	0.91	-3.08. 0.79	.226				
clustering coef.	-0.33	1.41	-3.33, 2.68	.820				
age	0.25	0.22	-0.22, 0.72	.269				
rank category	0.07	0.20	-0.37, 0.5	.754				
full reach:					51.16	3.57	0.074	7.49%
Intercept	-2.01	2.27	-6.85, 2.82	.389				
reach	1.00	2.58	-4.5, 6.51	.703				
age	0.25	0.21	-0.20, 0.71	.254				
rank category	0.05	0.20	-0.38, 0.49	.802				
null model:					47.59	0	0.440	7.11%
Intercept	-1.20	0.85	-3.00, 0.60	.178				
age	0.24	0.20	-0.2, 0.67	.261				
rank category	0.06	0.2	-0.35, 0.48	.751				

Table IV-III 12 Details on the full and null LMs regarding females' mean fGCM concentrations, using measures of affiliative network position as predictors (i.e. strength, eigenvector centrality, betweenness centrality, clustering coefficient, and reach). The network was based on dyadic CSI values. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	ΔAIC_C	**ω**	Marginal R^2
full strength:					277.47	0	0.356	48.81%
Intercept	3921.41	523.87	2804.80, 5038.01	<.0001				
strength	-15.38	7.56	-31.49, 0.73	.06				
age	-134.44	81.23	-307.57, 38.69	.119				
rank category	**-359.41**	**91.56**	**-554.56, -164.26**	**.001**				
full eigenvector centrality:					280.62	3.14	0.074	40.48%
Intercept	3389.22	447.91	2434.53, 4343.90	<.0001				
eigenvector cent.	-369.88	336.07	-1086.20, 346.44	.228				
age	-131.49	89.14	-321.48, 58.49	.161				
rank category	**-301.42**	**92.03**	**-497.57, -105.28**	**.005**				
full betweenness centrality:					278.22	0.75	0.244	46.92%
Intercept	3634.33	447.96	2679.52, 4589.15	<.0001				
betweenness	-8.96	4.86	-19.33, 1.40	.085				
age	-167.40	83.34	-345.04, 10.23	.063				
rank category	**-355.39**	**94.35**	**-556.49, 154.28**	**.002**				
full clustering coefficient:					281.2	3.73	0.055	38.83%
Intercept	3189.72	385.07	2368.96, 4010.48	<.0001				
clustering coef.	-509.91	598.79	-1786.01, 766.19	.408				
age	-124.30	93.28	-323.11, 74.51	.203				
rank category	**-260.36**	**86.36**	**-444.44, -76.29**	**.009**				
full reach:					281.81	4.34	0.041	37.06%
Intercept	2669.82	982.22	576.27, 4763.37	.016				
reach	537.67	1116.67	-1842.45, 2917.8	.637				
age	-138.96	92.35	-335.8, 57.88	.153				
rank category	**-268.78**	**88.62**	**-457.68, -79.88**	**.008**				
null model:					278.34	0.87	0.230	37.69%
Intercept	3106.25	369.18	2323.62, 3888.88	<.0001				
age	-147.11	88.58	-334.89, 40.67	.116				
rank category	**-262.65**	**85.58**	**-444.06, -81.24**	**.007**				

AFFILIATION NETWORK – PERMUTATION TESTS

Table IV-III 13 Details on the permutation procedure regarding the link between males’ demonstrated reactive scope measured as DRS and their clustering coefficient in an affiliative network. The network was based on dyadic CSI values, node permutations were repeated 1000 times. Models included rank category, while age was excluded due to VIFs > 2 between age and clustering coefficient.

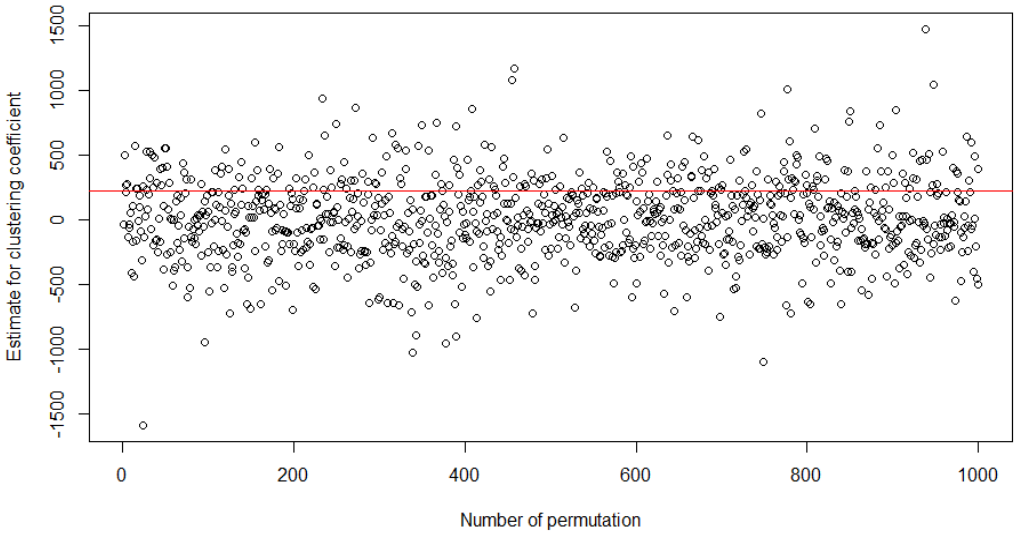
Network metric: clustering coefficient
Model: DRS ~ clustering coefficient + rank
Proportion observed est. < randomised est.: 0.277


Table IV-III 14 Details on the permutation procedure regarding the link between males’ mean fGCM concentrations and their betweenness centrality in an affiliative network. The network was based on dyadic CSI values, node permutations were repeated 1000 times. Models included age and rank category.

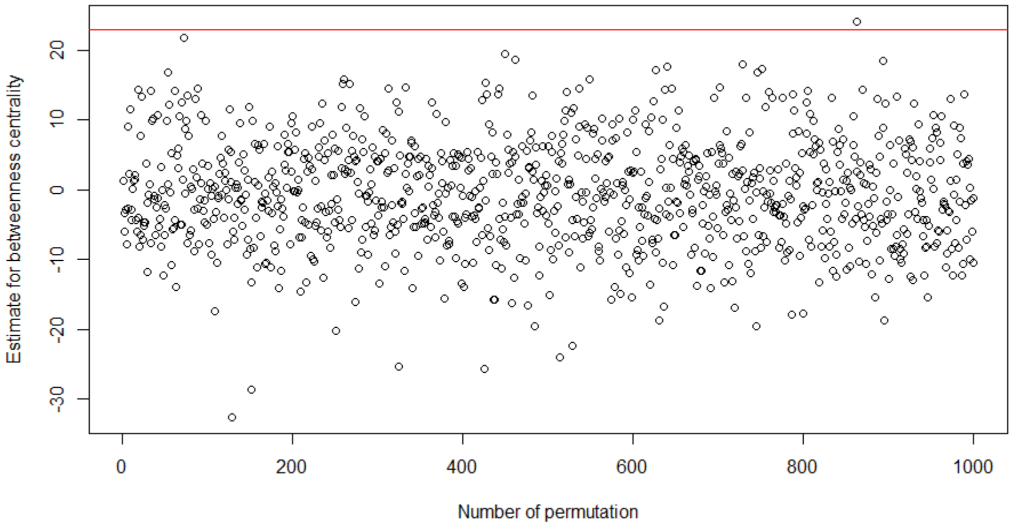
Network metric: betweenness centrality
Model: mean fGCM ~ betweenness centrality + age + rank
Proportion observed est. < randomised est.: 0.001


Table IV-III 15 Details on the permutation procedure regarding the link between males' mean fGCM concentrations and their clustering coefficient in an affiliative network. The network was based on dyadic CSI values, node permutations were repeated 1000 times. Models included rank category, while age was excluded due to VIFs > 2 between age and clustering coefficient.

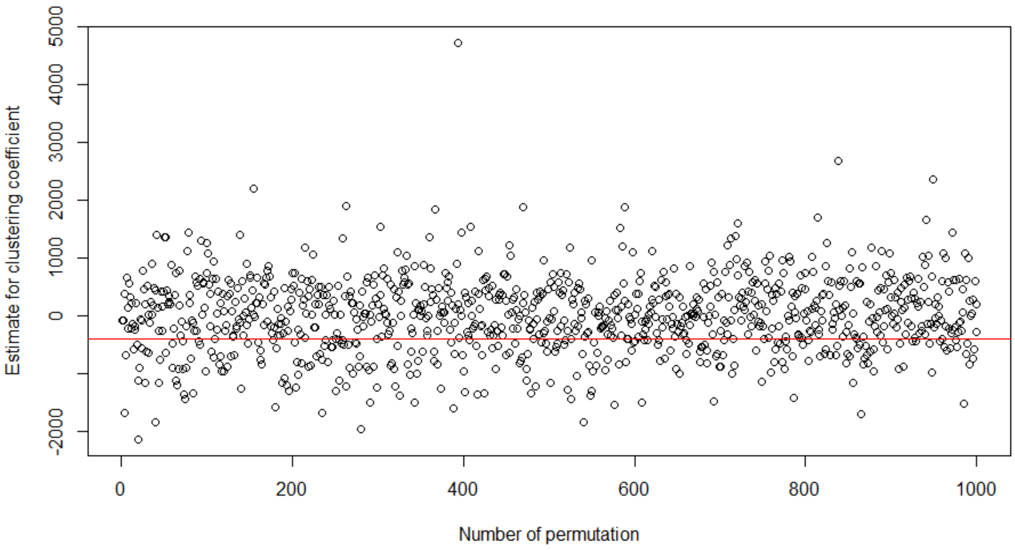
Network metric: clustering coefficient
Model: mean fGCM ~ clustering coefficient + rank
Proportion observed est. < randomised est.: 0.745


Table IV-III 16 Details on the permutation procedure regarding the link between females' demonstrated reactive scope measured as DRS$_{CV}$ and their clustering coefficient in an affiliative network. The network was based on dyadic CSI values, node permutations were repeated 1000 times. Models included age and rank category. DRS$_{CV}$ values were log$_2$-transformed to comply with model assumptions.

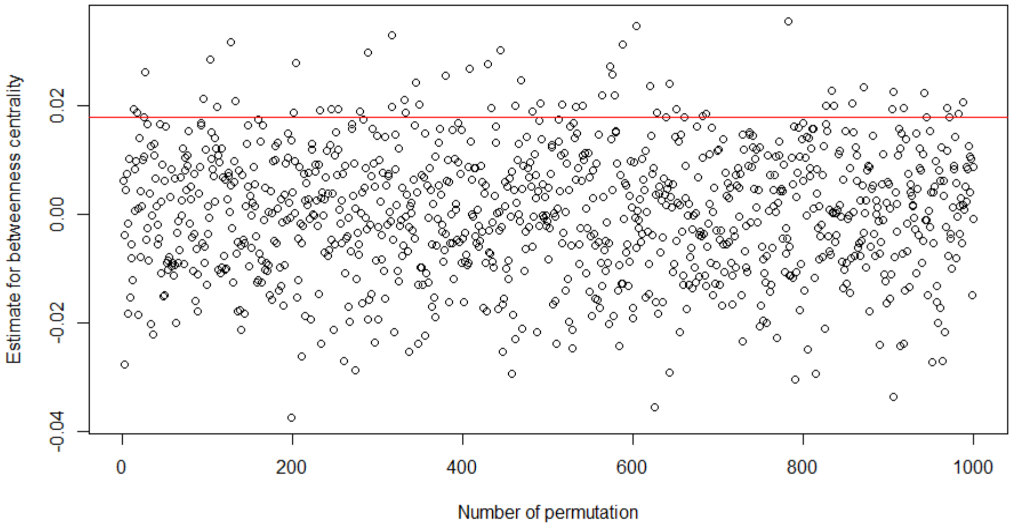
Network metric: betweenness centrality
Model: log$_2$(DRS$_{CV}$) ~ betweenness centrality + age + rank
Proportion observed est. < randomised est.: 0.06


Table IV-III 17 Details on the permutation procedure regarding the link between females' mean fGCM concentrations and their strength in an affiliative network. The network was based on dyadic CSI values, node permutations were repeated 1000 times. Models included age and rank category.

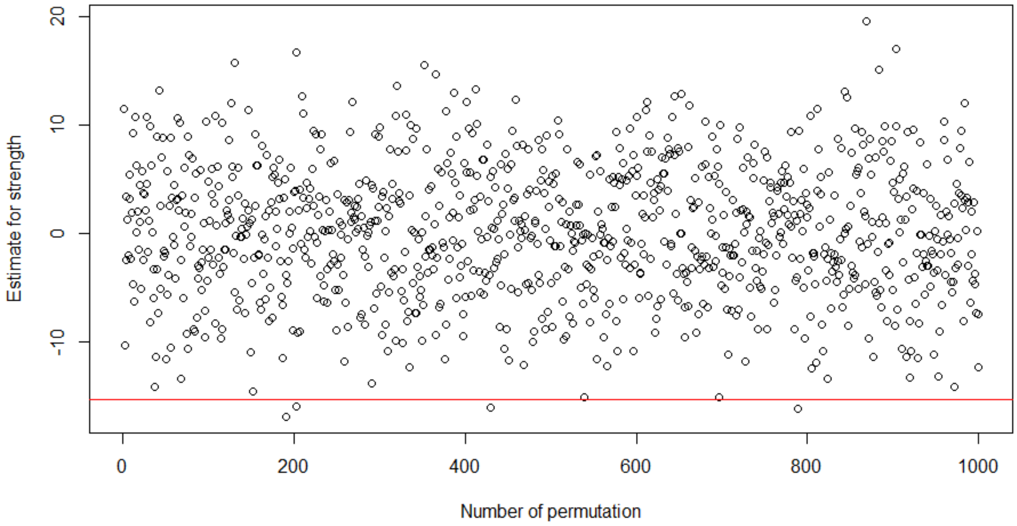
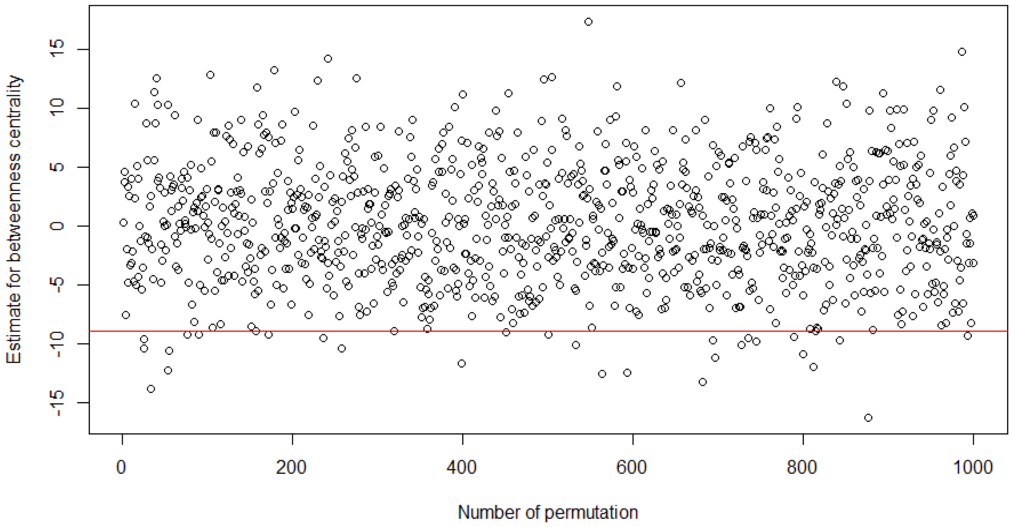
Network metric: strength
Model: mean fGCM ~ strength + age + rank
Proportion observed est. < randomised est.: 0.996


Table IV-III 18 Details on the permutation procedure regarding the link between females' mean fGCM concentrations and their betweenness centrality in an affiliative network. The network was based on dyadic CSI values, node permutations were repeated 1000 times. Models included age and rank category.

Network metric: betweenness centrality
Model: mean fGCM ~ betweenness centrality + age + rank
Proportion observed est. < randomised est.: 0.97


AGONISM NETWORK

Table IV-III 19 Details on the full and null LMs regarding males' demonstrated reactive scope measured as DRS, using measures of agonistic network position as predictors (i.e. strength, degree, eigenvector centrality, betweenness centrality, clustering coefficient, and reach). The undirected network was based on all agonistic interactions. Models included age and rank category. (VIFs between degree and rank were larger than 2, so rank was excluded here.)

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	**ω**	Marginal R^2
full strength:					152.26	3.8	0.068	48.81%
Intercept	344.33	244.51	-233.85, 922.50	.202				
strength	-78	43.14	-180.02, 24.02	.114				
age	45.04	36.76	-41.89, 131.97	.260				
rank category	9.68	51.99	-113.26, 132.62	.858				
full degree:					148.46	0	0.453	36.34%
Intercept	284.03	230.40	-247.27, 815.33	.253				
degree	-12.55	9.9	-35.38, 10.27	.240				
age	70.43	35.6	-11.66, 152.52	.083				
full eigenvector centrality:					151.3	2.84	0.109	52.48%
Intercept	314.82	206.10	-172.52, 802.17	.171				
eigenvector cent.	-382.82	186.63	-824.13, 58.5	.079				
age	41.48	35.38	-41.18, 125.13	.279				
rank category	21.44	46.76	-89.14, 132.02	.661				
full betweenness centrality:					154.19	5.73	0.026	40.75%
Intercept	86.03	158.55	-288.88, 460.94	.604				
betweenness	-7.2	5.66	-20.58, 6.18	.244				
age	43.11	40.56	-52.80, 139.02	.323				
rank category	29.12	53.75	-97.98, 156.21	.605				
full clustering coefficient:					155.73	7.27	0.012	33.58%
Intercept	497.92	804.02	-1403.27, 2399.12	.555				
clustering coef.	-876.47	1255.35	-3844.91, 2091.97	.508				
age	43.41	44.76	-62.43, 149.25	.364				
rank category	80.91	67.17	-77.91, 239.74	.267				
full reach:					156.00	7.54	0.010	32.28%
Intercept	184.26	451.86	-884.22, 1252.73	.696				
reach	-279.73	504.35	-1472.32, 912.87	.596				
age	48.62	43.89	-55.17, 152.41	.305				
rank category	40.49	59.18	-99.44, 180.43	.516				
null model:					149.14	0.68	0.322	32.80%
Intercept	-57.16	115.90	-324.42, 210.09	.635				
age	52.62	41.38	-42.79, 148.04	.239				
rank category	53.04	52.26	-67.47, 173.56	.340				

Table IV-III 20 Details on the full and null LMs regarding males' demonstrated reactive scope measured as DRS_{CV}, using measures of agonistic network position as predictors (i.e. strength, degree, eigenvector centrality, betweenness centrality, clustering coefficient, and reach). The undirected network was based on all agonistic interactions. Models included age and rank category. (VIFs between degree and rank were larger than 2, so rank was excluded here.)

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	**ω**	Marginal R^2
full strength:					19.05	2.5	0.121	41.3%
Intercept	1.53	0.57	0.17, 2.88	.032				
strength	-0.24	0.10	-0.48, 0.003	.052				
age	0.04	0.09	-0.16, 0.24	.657				
rank category	-0.07	0.12	-0.36, 0.22	.577				
full degree:					18.04	1.49	0.200	9.31%
Intercept	0.66	0.61	-0.76, 2.07	.316				
degree	-0.01	0.03	-0.07, 0.05	.651				
age	0.08	0.09	-0.14, 0.30	.404				

full eigenvector centrality:					16.55	0	0.423	51.5%
Intercept	1.48	0.45	0.41, 2.54	.014				
eigenvector cent.	**-1.20**	**0.41**	**-2.17, -0.24**	**.022**				
age	0.03	0.08	-0.15, 0.21	.728				
rank category	-0.04	0.10	-0.28, 0.20	.715				
full betweenness centrality:					21.17	4.62	0.042	31.36%
Intercept	0.79	0.38	-0.1, 1.68	.073				
betweenness	-0.02	0.02	-0.06, 0.01	.113				
age	0.03	0.1	-0.2, 0.26	.756				
rank category	-0.02	0.13	-0.32, 0.28	.877				
full clustering coefficient:					23.94	7.39	0.010	16.61%
Intercept	2.29	2.01	-2.47, 7.05	.293				
clustering coef.	-3.13	3.14	-10.55, 4.30	.353				
age	0.03	0.11	-0.23, 0.3	.795				
rank category	0.16	0.17	-0.24, 0.56	.374				
full reach:					24.97	8.42	0.006	10.63%
Intercept	0.90	1.17	-1.86, 3.67	.466				
reach	-0.69	1.31	-3.78, 2.40	.615				
age	0.05	0.11	-0.22, 0.32	.654				
rank category	0.03	0.15	-0.33, 0.39	.853				
null model:					18.07	1.52	0.198	9.11%
Intercept	0.31	0.3	-0.38, 1.00	.331				
age	0.06	0.11	-0.18, 0.31	.572				
rank category	0.06	0.14	-0.25, 0.37	.667				

Table IV-III 21 Details on the full and null LMs regarding males' mean fGCM concentrations, using measures of agonistic network position as predictors (i.e. strength, degree, eigenvector centrality, betweenness centrality, clustering coefficient, and reach). The undirected network was based on all agonistic interactions. Models included age and rank category. (VIFs between degree and rank were larger than 2, so rank was excluded here.)

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	$\Delta\ \text{AIC}_C$	ω	Marginal R^2
full strength:					174.44	7.69	0.011	19.56%
Intercept	2110.77	670.26	525.86, 3695.68	.016				
strength	33.41	118.27	-246.24, 313.07	.786				
age	-4.94	100.78	-243.24, 233.35	.962				
rank category	-148.37	142.52	-485.38, 188.64	.333				
full degree:					166.75	0	0.527	23.91%
Intercept	1297.73	529.09	77.65, 2517.80	.04				
degree	35.38	22.73	-17.03, 87.78	.158				
age	-64.75	81.75	-253.27, 123.76	.451				
full eigenvector centrality:					174.56	7.81	0.011	18.94%
Intercept	2234.11	593.22	831.37, 3636.84	.007				
eigenvector cent.	50.07	537.19	-1220.17, 1320.32	.928				
age	-6.73	101.83	-247.53, 234.06	.949				
rank category	-162.81	134.61	-481.10, 155.48	.266				
full betweenness centrality:					174.52	7.77	0.011	19.16%
Intercept	2334.98	399.47	1390.38, 3279.57	.0006				
betweenness	-2.63	14.26	-36.33, 31.09	.859				
age	-11.66	102.2	-253.31, 229.99	.912				
rank category	-175.67	135.43	-495.90, 144.56	.236				
full clustering coefficient:					174.52	7.77	0.011	19.13%
Intercept	1956.26	1888.62	-2509.01, 6422.12	.335				
clustering coef.	515.54	2948.79	-6457.24, 7488.32	.866				
age	-2.77	105.14	-251.39, 245.85	.980				
rank category	-183.34	157.78	-556.43, 189.75	.283				

full reach:					173.59	6.84	0.017	24.2%
Intercept	1501.41	1005.16	-875.40, 3878.23	.179				
reach	905.32	1121.92	-1747.59, 3558.24	.446				
age	4.78	97.64	-226.10, 235.65	.962				
rank category	-126.33	131.64	-437.61, 184.95	.369				
null model:					167.24	0.49	0.412	20.99%
Intercept	2282.76	263.80	1674.44, 2891.09	<.0001				
age	-8.19	94.18	-225.38, 209	.933				
rank category	-166.95	118.96	-441.26, 107.37	.198				

Table IV-III 22 Details on the full and null LMs regarding females' demonstrated reactive scope measured as DRS, using measures of agonistic network position as predictors (i.e. strength, degree, eigenvector centrality, betweenness centrality, clustering coefficient, and reach). The undirected network was based on all agonistic interactions. Models included age and rank category. DRS values were log$_2$-transformed to comply with model assumptions.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	ω	Marginal R^2
full strength:					75.13	3.06	0.069	5.91%
Intercept	10.78	3.26	3.83, 17.73	.005				
strength	-0.6	0.57	-1.82, 0.63	.315				
age	-0.05	0.41	-0.93, 0.84	.914				
rank category	-0.40	0.53	-1.54, 0.73	.461				
full degree:					72.80	0.73	0.222	15.22%
Intercept	13.63	3.59	5.97, 21.3	.002				
degree	-0.22	0.13	-0.49, 0.04	.095				
age	-0.03	0.38	-0.83, 0.77	.937				
rank category	-0.29	0.39	-1.13, 0.54	.462				
full eigenvector centrality:					75.59	3.52	0.055	3.96%
Intercept	10.02	3.09	3.43, 16.61	.006				
eigenvector cent.	-2.68	3.22	-9.54, 4.18	.419				
age	-0.03	0.42	-0.94, 0.87	.938				
rank category	-0.32	0.53	-1.45, 0.81	.556				
full betweenness centrality:					72.07	0	0.320	17.97%
Intercept	9.83	1.82	5.95, 13.70	<.0001				
betweenness	-0.09	0.05	-0.19, 0.01	.068				
age	0.03	0.36	-0.74, 0.81	.929				
rank category	-0.47	0.42	-1.36, 0.43	.282				
full clustering coefficient:					76.11	4.04	0.042	1.72%
Intercept	10.75	5.85	-1.72, 23.22	.986				
clustering coef.	-4.35	8.40	-22.26, 13.56	.612				
age	0.06	0.41	-0.81, 0.93	.891				
rank category	-0.03	0.39	-0.86, 0.81	.945				
full reach:					75.58	3.51	0.056	4.02%
Intercept	6.38	2.41	1.24, 11.53	.018				
reach	1.36	1.62	-2.1, 4.82	.414				
age	0.13	0.40	-0.73, 0.99	.746				
rank category	0.15	0.43	-0.77, 1.07	.737				
null model:					72.69	0.62	0.235	0.28%
Intercept	7.85	1.65	4.36, 11.34	.0002				
age	0.08	0.4	-0.75, 0.92	.836				
rank category	-0.02	0.38	-0.83, 0.79	.965				

Table IV-III 23 Details on the full and null LMs regarding females' demonstrated reactive scope measured as DRS_{CV}, using measures of agonistic network position as predictors (i.e. strength, degree, eigenvector centrality, betweenness centrality, clustering coefficient, and reach). The undirected network was based on all agonistic interactions. Models included age and rank category. DRS_{CV} values were log_2-transformed to comply with model assumptions.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	ω	Marginal R^2
full strength:					50.71	3.12	0.071	9.3%
Intercept	-0.14	1.72	-3.80, 3.51	.935				
strength	-0.22	0.30	-0.86, 0.43	.487				
age	0.19	0.22	-0.27, 0.65	.393				
rank category	-0.08	0.28	-0.67, 0.52	.790				
full degree:					48.29	0.7	0.239	18.69%
Intercept	1.56	1.89	-2.46, 5.58	.423				
degree	-0.11	0.07	-0.25, 0.03	.126				
age	0.18	0.2	-0.24, 0.60	.367				
rank category	-0.07	0.21	-0.51, 0.37	.742				
full eigenvector centrality:					50.64	3.05	0.074	9.60%
Intercept	-0.18	1.60	-3.6, 3.24	.912				
eigenvector cent.	-1.26	1.67	-4.82, 2.3	.462				
age	0.18	0.22	-0.28, 0.65	.417				
rank category	-0.08	0.27	-0.66, 0.51	.779				
full betweenness centrality:					49.24	1.65	0.149	15.12%
Intercept	-0.47	1	-2.6, 1.66	.644				
betweenness	-0.03	0.03	-0.09, 0.02	.204				
age	0.22	0.20	-0.21, 0.65	.290				
rank category	-0.10	0.23	-0.59, 0.39	.660				
full clustering coefficient:					51.25	3.66	0.054	7.08%
Intercept	-0.41	3.04	-6.9, 6.07	.894				
clustering coef.	-1.18	4.37	-10.49, 8.13	.790				
age	0.23	0.21	-0.22, 0.68	.294				
rank category	0.06	0.20	-0.37, 0.49	.769				
full reach:					50.60	3.01	0.075	9.74%
Intercept	-1.90	1.25	-4.57, 0.76	.149				
reach	0.65	0.84	-1.14, 2.44	.451				
age	0.26	0.21	-0.18, 0.71	.230				
rank category	0.14	0.22	-0.34, 0.62	.535				
null model:					47.59	0	0.339	7.11%
Intercept	-1.20	0.85	-3.00, 0.60	.178				
age	0.24	0.20	-0.2, 0.67	.261				
rank category	0.06	0.2	-0.35, 0.48	.751				

Table IV-III 24 Details on the full and null LMs regarding females' mean fGCM concentrations, using measures of agonistic network position as predictors (i.e. strength, degree, eigenvector centrality, betweenness centrality, clustering coefficient, and reach). The undirected network was based on all agonistic interactions. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	ω	Marginal R^2
full strength:					281.89	3.55	0.068	36.79%
Intercept	3367.56	752.57	1763.5, 4971.62	.0004				
strength	-53.19	132.31	-335.2, 228.82	.693				
age	-158.62	95.39	-361.95, 44.70	.117				
rank category	**-297.13**	**122.81**	**-558.90, -35.36**	**.029**				
full degree:					282.09	3.75	0.062	36.21%
Intercept	3041.68	886.32	1152.54, 4930.82	.004				
degree	2.50	30.99	-63.54, 68.55	.937				
age	-154.85	92.80	-343.64, 51.95	.137				
rank category	**-259.55**	**96.36**	**-464.94, -54.16**	**.017**				

full eigenvector centrality:					281.68	3.34	0.076	37.42%
Intercept	3446.02	701.16	1951.53, 4940.51	.0002				
eigenvector cent.	-419.50	729.79	-1975.00, 1136.01	.574				
age	-165.37	95.91	-369.8, 39.05	.105				
rank category	**-309.05**	**120.06**	**-565.86, -54.05**	**.021**				
full betweenness centrality:					281.74	3.4	0.074	37.24%
Intercept	3239.14	452.91	2273.79, 4204.48	<.0001				
betweenness	-6.13	11.53	-30.72, 18.45	.602				
age	-150.48	90.86	-344.13, 43.17	.118				
rank category	**-293**	**104.51**	**-515.75, -70.24**	**.013**				
full clustering coefficient:					279.26	0.92	0.255	44.21%
Intercept	1279.75	1227.31	-1336.19, 3895.69	.314				
clustering coef.	2739.55	1762.65	-1017.45, 6496.54	.141				
age	-130.59	85.57	-312.97, 51.79	.148				
rank category	**-256.07**	**82.13**	**-431.13, -81.01**	**.007**				
full reach:					282.08	3.74	0.062	36.23%
Intercept	3064.35	553.03	1885.6, 4243.11	<.0001				
reach	38.88	371.82	-753.64, 831.41	.918				
age	-145.68	92.47	-342.77, 51.40	.136				
rank category	**-257.95**	**99.13**	**-469.25, -46.66**	**.020**				
null model:					278.34	0	0.404	37.69%
Intercept	3106.25	369.18	2323.62, 3888.88	<.0001				
age	-147.11	88.58	-334.89, 40.67	.116				
rank category	**-262.65**	**85.58**	**-444.06, -81.24**	**.007**				

AGONISM NETWORK – PERMUTATION TESTS

Table IV-III 25 Details on the permutation procedure regarding the link between males' demonstrated reactive scope measured as DRS and their degree in an agonistic network. The undirected network was based on all agonistic interactions, node permutations were repeated 1000 times. Models included age, while rank category was excluded due to VIFs > 2 between rank and degree.

Network metric: degree

Model: DRS ~ degree + age

Proportion observed est. < randomised est.: 0.839

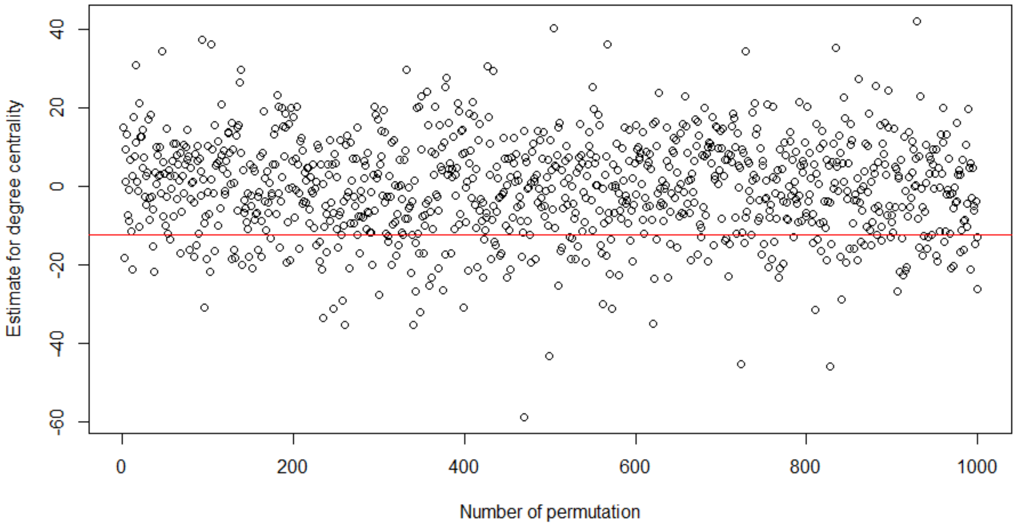


Table IV-III 26 Details on the permutation procedure regarding the link between males' demonstrated reactive scope measured as DRS and their eigenvector centrality in an agonistic network. The undirected network was based on all agonistic interactions, node permutations were repeated 1000 times. Models included age and rank category.

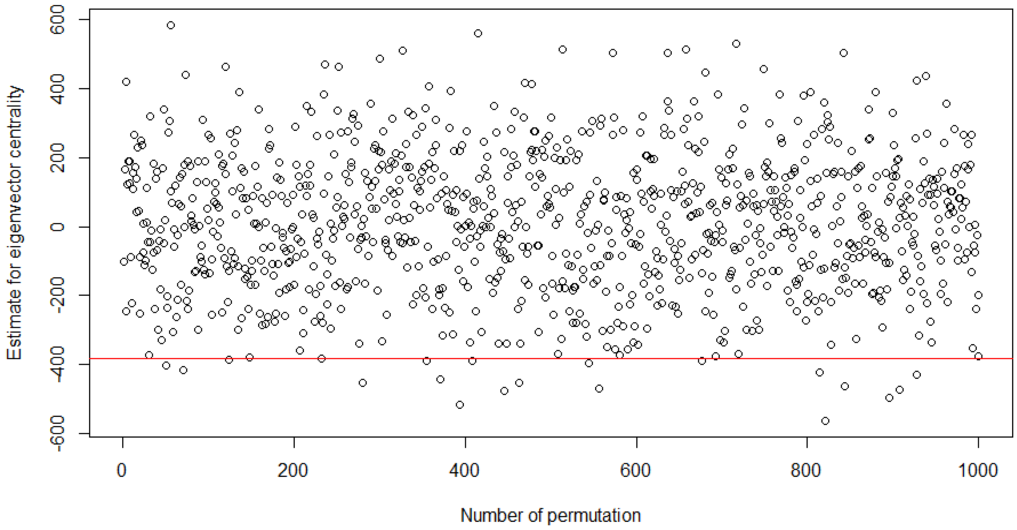
Network metric: eigenvector centrality
Model: DRS ~ eigenvector centrality + age + rank
Proportion observed est. < randomised est.: 0.98


Table IV-III 27 Details on the permutation procedure regarding the link between males' demonstrated reactive scope measured as DRS_{CV} and their degree in an agonistic network. The undirected network was based on all agonistic interactions, node permutations were repeated 1000 times. Models included age, while rank category was excluded due to VIFs > 2 between rank and degree.

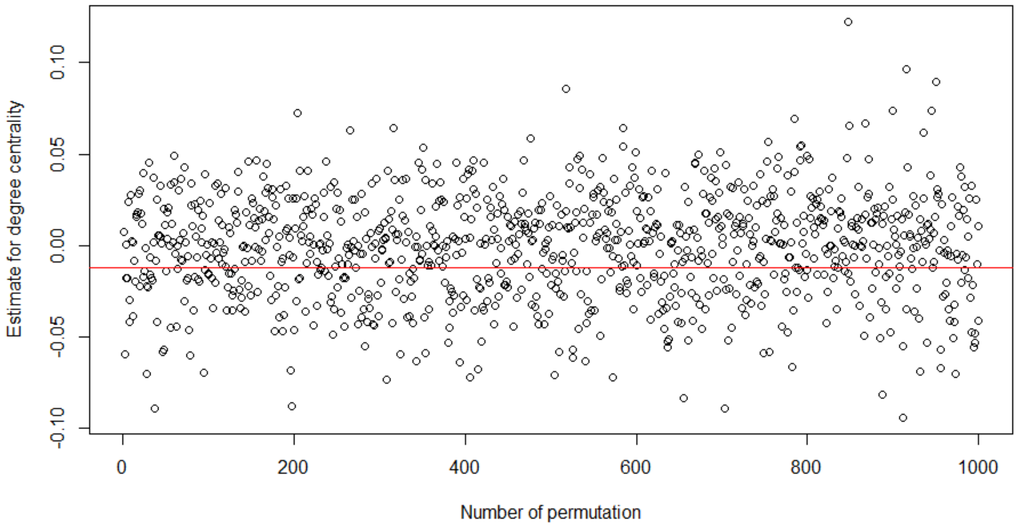
Network metric: degree
Model: DRS_{CV} ~ degree + age
Proportion observed est. < randomised est.: 0.681


Table IV-III 28 Details on the permutation procedure regarding the link between males' demonstrated reactive scope measured as DRS$_{CV}$ and their eigenvector centrality in an agonistic network. The undirected network was based on all agonistic interactions, node permutations were repeated 1000 times. Models included age and rank category.

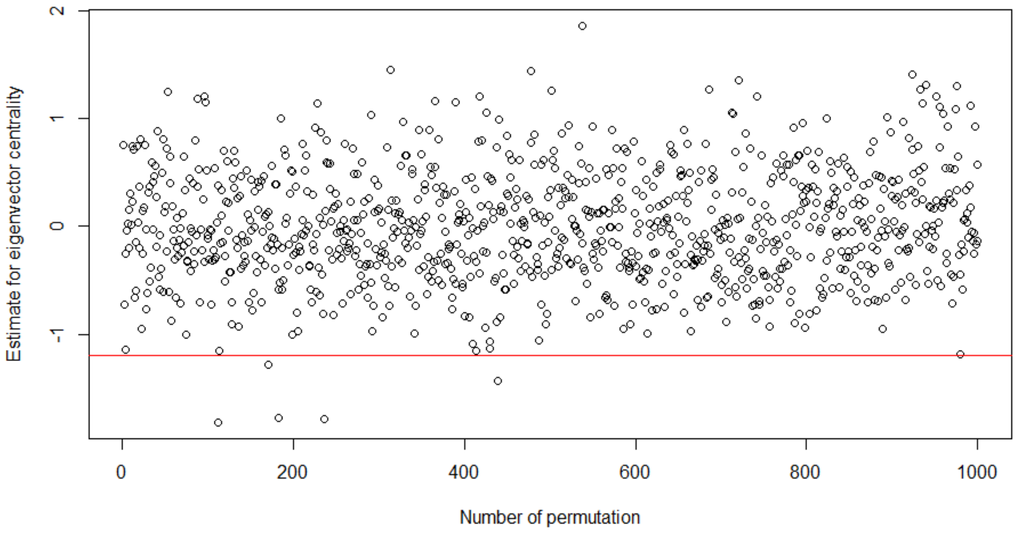
Network metric: eigenvector centrality
Model: DRS$_{CV}$ ~ eigenvector centrality + age + rank
Proportion observed est. < randomised est.: 0.995


Table IV-III 29 Details on the permutation procedure regarding the link between males' mean fGCM concentrations and their degree in an agonistic network. The undirected network was based on all agonistic interactions, node permutations were repeated 1000 times. Models included age, while rank category was excluded due to VIFs > 2 between rank and degree.

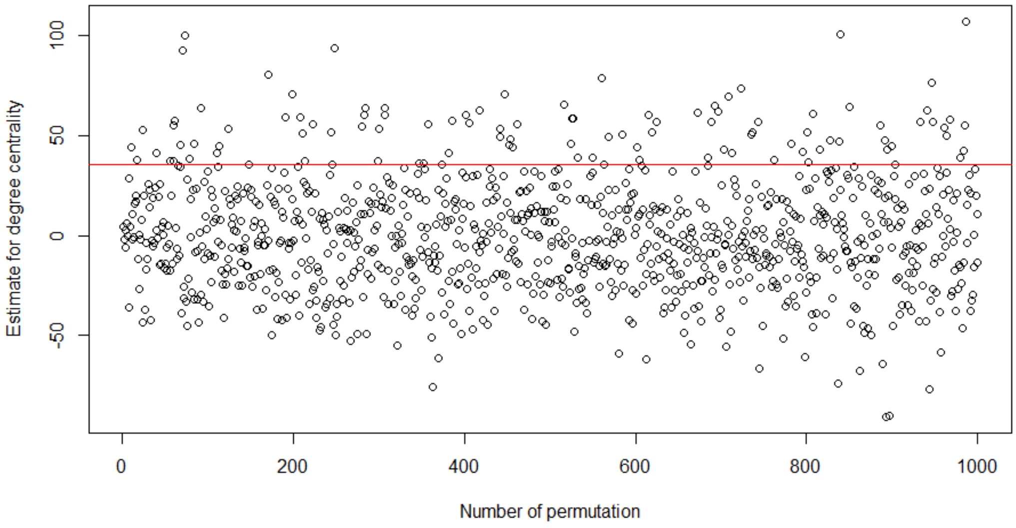
Network metric: degree
Model: mean fGCM ~ degree + age
Proportion observed est. < randomised est.: 0.104


Table IV-III 30 Details on the permutation procedure regarding the link between females' demonstrated reactive scope measured as DRS and their degree in an agonistic network. The undirected network was based on all agonistic interactions, node permutations were repeated 1000 times. Models included age and rank category. DRS values were $\log_2$-transformed to comply with model assumptions.

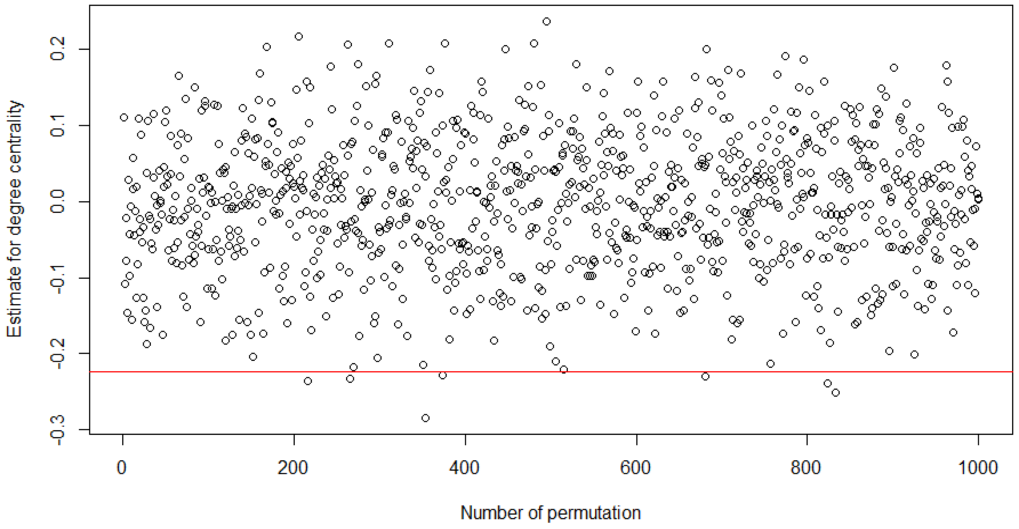
Network metric: degree
Model: $\log_2(\mathrm{DRS})$ ~ degree + age + rank
Proportion observed est. < randomised est.: 0.993


Table IV-III 31 Details on the permutation procedure regarding the link between females' demonstrated reactive scope measured as DRS and their betweenness centrality in an agonistic network. The undirected network was based on all agonistic interactions, node permutations were repeated 1000 times. Models included age and rank category. DRS values were $\log_2$-transformed to comply with model assumptions.

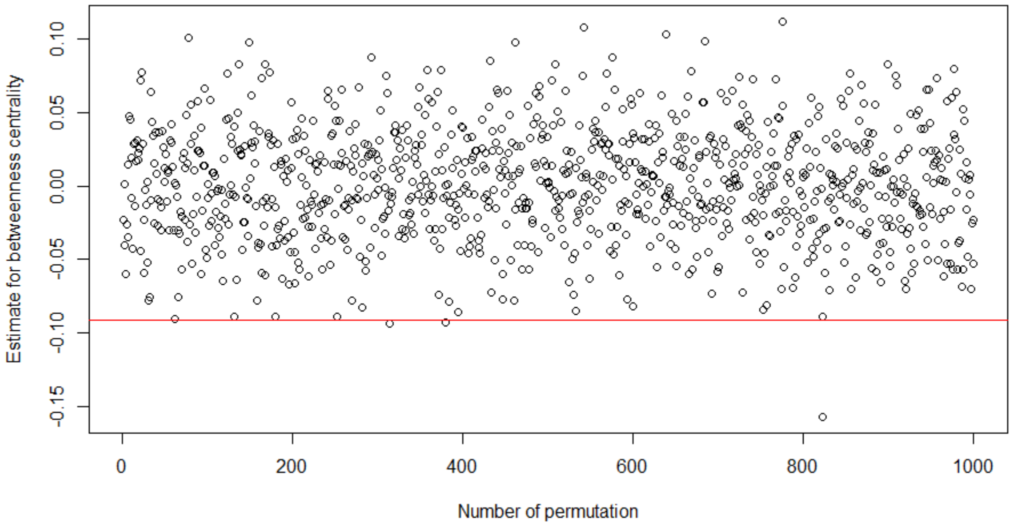
Network metric: betweenness centrality
Model: $\log_2(\mathrm{DRS})$ ~ betweenness centrality + age + rank
Proportion observed est. < randomised est.: 0.997


Table IV-III 32 Details on the permutation procedure regarding the link between females' demonstrated reactive scope measured as DRS_{CV} and their degree in an agonistic network. The undirected network was based on all agonistic interactions, node permutations were repeated 1000 times. Models included age and rank category. DRS_{CV} values were log_2-transformed to comply with model assumptions.

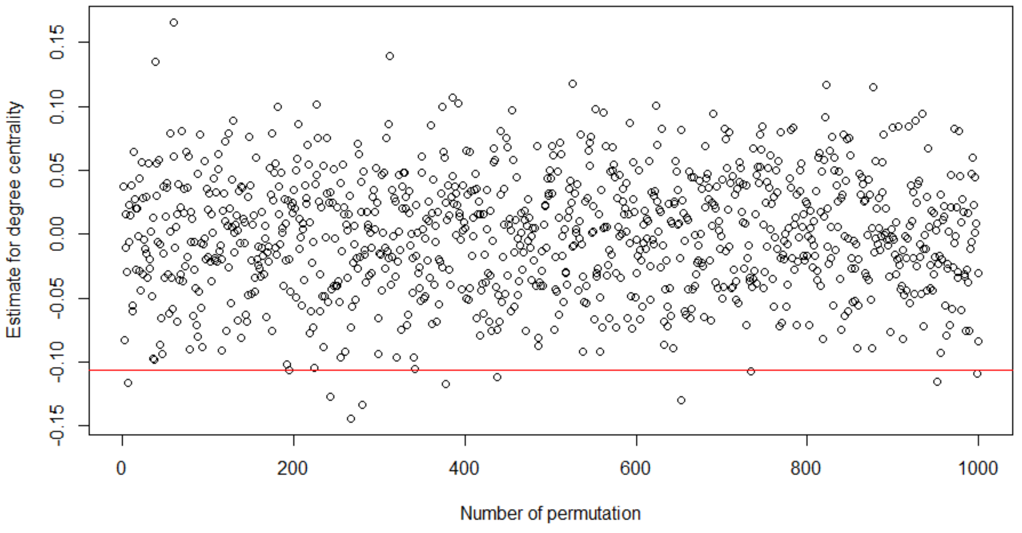
Network metric: degree
Model: $log_2(DRS_{CV})$ ~ degree + age + rank
Proportion observed est. < randomised est.: 0.99


Table IV-III 33 Details on the permutation procedure regarding the link between females' demonstrated reactive scope measured as DRS_{CV} and their betweenness centrality in an agonistic network. The undirected network was based on all agonistic interactions, node permutations were repeated 1000 times. Models included age and rank category. DRS_{CV} values were log_2-transformed to comply with model assumptions.

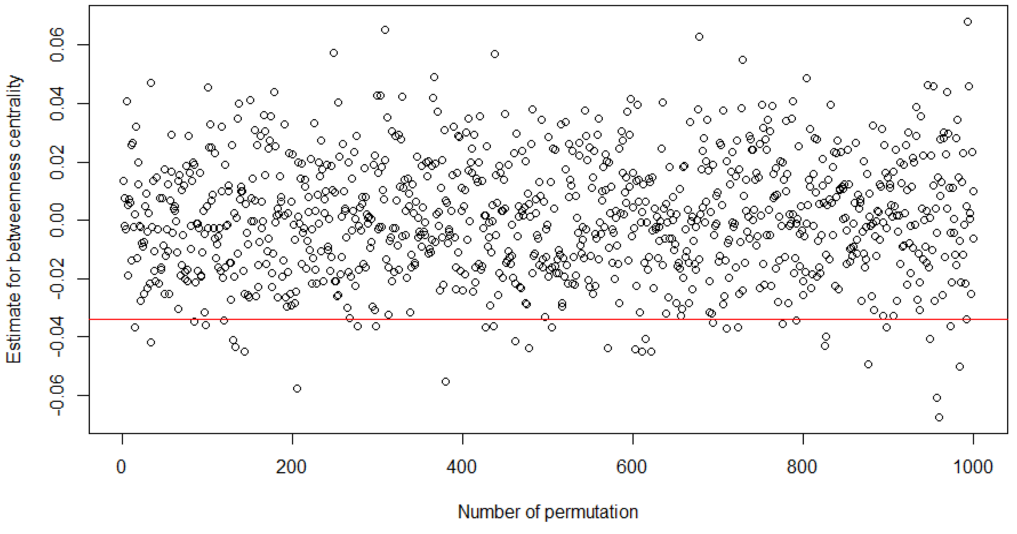
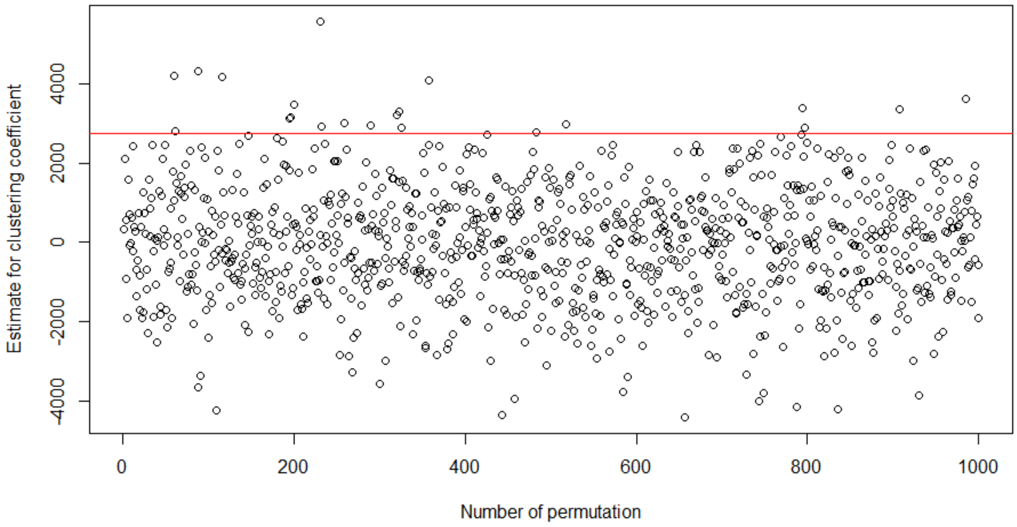
Network metric: betweenness centrality
Model: $log_2(DRS_{CV})$ ~ betweenness centrality + age + rank
Proportion observed est. < randomised est.: 0.963


Table IV-III 34 Details on the permutation procedure regarding the link between females' mean fGCM concentrations and their clustering coefficient in an agonistic network. The undirected network was based on all agonistic interactions, node permutations were repeated 1000 times. Models included age and rank category.

Network metric: clustering coefficient
Model: mean fGCM ~ clustering coefficient + age + rank
Proportion observed est. < randomised est.: 0.021


Appendix V – Resilience

Appendix V – I Coat condition exploration

Table A V-I 1 Details on the full and null LMM regarding females' coat condition ratings, using their reproductive state at the time as predictor. Models included age and rank category. Individual ID was included as random factor.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2	Cond. R^2
full model:					204.13	0	0.911	26.47%	56.12%
Intercept	7.56	0.59	6.33, 8.74	<.0001					
cycling - lactating	**0.97**	**0.32**	**0.35, 1.62**	**.003**					
cycling - pregnant	**0.86**	**0.31**	**0.26, 1.47**	**.006**					
lactating - pregnant	-0.11	0.16	-0.43, 0.21	.488					
age	**-0.34**	**0.13**	**-0.61, -0.07**	**.019**					
rank	-0.07	0.13	-0.34, 0.21	.606					
null model:					208.79	4.66	0.089	16.45%	50.51%
Intercept	8.74	0.47	7.77, 9.72	<.0001					
age	**-0.34**	**0.14**	**-0.62, -0.06**	**.023**					
rank	-0.19	0.13	-0.46, 0.08	.166					

Table A V-I 2 Details on the full and null LMs regarding males' average coat condition, using rank category and mean randomised Elo-rating as predictors. Models included age.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2
full model:					15.27	2.6	0.158	34.51%
Intercept	9.03	0.26	8.42, 9.64	<.0001				
rank category	-0.18	0.12	-0.45, 0.1	.179				
age	-0.08	0.09	-0.30, 0.13	.404				
full model:					14.24	1.57	0.264	39.66%
Intercept	8.09	0.44	7.07, 9.11	<.0001				
rand. Elo	0.001	0.0003	-0.0002, 0.001	.113				
age	-0.09	0.09	-0.29, 0.11	.343				
null model:					12.67	0	0.578	21.52%
Intercept	8.79	0.22	8.29, 9.3	<.0001				
age	-0.15	0.09	-0.35, 0.05	.132				

Table A V-I 3 Details on the full and null LMs regarding females' average coat condition, using rank category and mean randomised Elo-rating as predictors. Models included age.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2
full model:					35.74	1.29	0.249	25.52%
Intercept	8.74	0.51	7.65, 9.83	<.0001				
rank category	-0.19	0.14	-0.5, 0.12	.205				
age	**-0.34**	**0.15**	**-0.66, -0.02**	**.037**				
full model:					35.54	1.2	0.275	26.23%
Intercept	7.62	0.51	6.54, 8.70	<.0001				
rand. Elo	0.001	0.001	-0.0003, 0.002	.184				
age	**-0.35**	**0.15**	**-0.67, -0.03**	**.033**				
null model:					34.45	0	0.475	19.05%
Intercept	8.19	0.31	7.54, 8.85	<.0001				
age	-0.31	0.15	-0.63, 0.01	.055				

Table A V-I 4 Details on the full and null LMs regarding males' relative change in coat condition, using rank category and mean randomised Elo-rating as predictors. Models included age.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2
full model:					90.06	4.43	0.088	13.5%
Intercept	-13.02	7.90	-31.25, 5.20	.138				
rank category	2.78	3.56	-5.44, 11.00	.457				
age	1.42	2.82	-5.08, 7.93	.628				

full model:					89.70	4.07	0.105	15.83%
Intercept	2.27	13.64	-29.2, 33.73	.872				
rand. Elo	-0.01	0.01	-0.03, 0.01	.371				
age	1.46	2.67	-4.71, 7.62	.601				
null model:					85.63	0	0.806	9.04%
Intercept	-9.27	6.13	-23.14, 4.60	.165				
age	2.44	2.45	-3.1, 7.98	.345				

Table A V-I 5 Details on the full and null LMs regarding females' relative change in coat condition, using rank category and mean randomised Elo-rating as predictors. Models included age.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2
full model:					165.28	0.5	0.288	16.45%
Intercept	-27.89	15.55	-60.85, 5.07	.092				
rank category	6.90	4.37	-2.36, 16.16	.134				
age	5.65	4.52	-3.93, 15.24	.229				
full model:					164.95	0.17	0.341	17.78%
Intercept	12.81	15.38	-19.80, 45.42	.417				
rand. Elo	-0.02	0.01	-0.05, 0.01	.112				
age	5.95	4.50	-3.60, 15.5	.205				
null model:					164.78	0	0.371	5.08%
Intercept	-8.05	9.57	-28.23, 12.13	.412				
age	4.58	4.66	-5.26, 14.41	.340				

Table A V-I 6 Details on the full and null LMs regarding males' delta coat temperature, using rank category and mean randomised Elo-rating as predictors. Models included age.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2
full model:					48.55	4.46	0.089	5.54%
Intercept	3.14	1.2	0.38, 5.9	.031				
rank category	0.41	0.54	-0.83, 1.66	.467				
age	-0.17	0.43	-1.15, 0.82	.703				
full model:					48.85	4.76	0.077	3.46%
Intercept	4.83	2.13	-0.08, 9.74	.053				
rand. Elo	-0.001	0.002	-0.004, 0.003	.567				
age	-0.11	0.42	-1.08, 0.85	.791				
null model:					44.09	0	0.833	0.02%
Intercept	3.69	0.93	1.6, 5.79	.003				
age	-0.02	0.37	-0.86, 0.82	.963				

Table A V-I 7 Details on the full and null LMs regarding females' delta coat temperature, using rank category and mean randomised Elo-rating as predictors. Models included age.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2
full model:					68.84	3.54	0.129	2.49%
Intercept	5.57	2.15	0.88, 10.26	.024				
rank category	-0.31	0.66	-1.74, 1.12	.645				
age	-0.24	0.58	-1.5, 1.02	.689				
full model:					69.09	3.79	0.114	1.09%
Intercept	4.44	2.20	-0.36, 9.24	.067				
rand. Elo	0.0003	0.002	-0.004, 0.01	.887				
age	-0.22	0.58	-1.5, 1.05	.712				
null model:					65.3	0	0.757	1.01%
Intercept	4.71	1.14	2.26, 7.17	.001				
age	-0.21	0.56	-1.42, 1	.711				

Table A V-I 8 Details on the full and null LMs regarding males' coat condition measures (average coat condition, relative change in coat condition, and mean delta coat temperature), using DRS and DRS$_{CV}$ as predictor. Models included age and mean randomised Elo-rating.

Fixed effect	estimate	SE	95 % - CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2
average coat condition:								
full DRS$_{CV}$:					21.52	7.27	0.025	36.77 %
Intercept	8.14	0.54	6.86, 9.42	<.0001				
DRS$_{CV}$	-0.06	0.33	-0.84, 0.72	.857				
age	-0.08	0.09	-0.31, 0.14	.399				
rand. Elo	0.001	0.0004	-0.0003, 0.001	.171				
full DRS:					21.55	7.31	0.025	36.59 %
Intercept	8.11	0.51	6.90, 9.32	<.0001				
DRS	-0.0001	0.001	-0.002, 0.002	.920				
age	-0.08	0.10	-0.33, 0.16	.449				
rand. Elo	0.001	0.0004	-0.0003, 0.001	.182				
null model:					14.24	0	0.951	39.66 %
Intercept	8.09	0.44	7.07, 0.11	<.0001				
age	-0.09	0.09	-0.29, 0.11	.343				
rand. Elo	0.001	0.0003	-0.0002, 0.001	.113				
relative change in coat condition:								
full DRS$_{CV}$:					97.03	7.33	0.024	14.17 %
Intercept	2.83	16.78	-36.84, 42.51	.871				
DRS$_{CV}$	-0.7	10.20	-24.82, 23.43	.947				
age	1.49	2.9	-5.37, 8.35	.623				
rand. Elo	-0.01	0.01	-0.04, 0.02	.417				
full DRS:					97.02	7.32	0.024	14.19 %
Intercept	2.79	15.83	-34.63, 40.22	.865				
DRS	-0.002	0.03	-0.06, 0.06	.935				
age	1.57	3.17	-5.93, 9.08	.635				
rand. Elo	-0.01	0.01	-0.04, 0.02	.426				
null model:					89.70	0	0.951	15.83 %
Intercept	2.27	13.64	-29.2, 33.73	.872				
age	1.46	2.67	-4.71, 7.62	.601				
rand. Elo	-0.01	0.01	-0.03, 0.01	.371				
mean delta coat temperature:								
full DRS$_{CV}$:					53.86	5.01	0.073	16.87 %
Intercept	-3.33	2.36	-8.91, 2.24	.200				
DRS$_{CV}$	-1.84	1.43	-5.23, 1.55	.241				
age	0.20	0.41	-0.76, 1.17	.631				
rand. Elo	0.0003	0.002	-0.003, 0.004	.858				
full DRS:					55.19	6.34	0.037	9.11 %
Intercept	-4.08	2.36	-9.67, 1.51	.128				
DRS	-0.003	0.004	-0.01, 0.01	.444				
age	0.28	0.47	-0.84, 1.40	.570				
rand. Elo	0.0004	0.002	-0.004, 0.004	.845				
null model:					48.85	0	0.890	3.46 %
Intercept	-4.83	2.13	-9.74, 0.08	.053				
age	0.11	0.42	-0.85, 1.08	.791				
rand. Elo	0.001	0.002	-0.003, 0.004	.567				

Table A V-I 9 Details on the full and null LMs regarding females' coat condition measures (average coat condition, relative change in coat condition, and mean delta coat temperature), using DRS and DRS$_{CV}$ as predictor. Models included age and mean randomised Elo-rating.

Fixed effect	estimate	SE	95 % - CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2
average coat condition:								
full DRS$_{CV}$:					37.93	2.39	0.208	29.6 %
Intercept	7.48	0.53	6.36, 8.60	<.0001				
DRS$_{CV}$	0.28	0.26	-0.28, 0.84	.307				
age	**-0.41**	**0.16**	**-0.75, -0.07**	**.022**				
rand. Elo	0.001	0.0005	-0.0003, 0.002	.18				

full DRS:					39.26	3.72	0.107	25.12 %
Intercept	7.63	0.53	6.50, 8.75	<.0001				
DRS	0.00004	0.0003	-0.001, 0.001	.87				
age	**-0.35**	**0.16**	**-0.69, -0.02**	**.041**				
rand. Elo	0.001	0.0005	-0.0004, 0.002	.209				
null model:					35.54	0	0.686	26.23 %
Intercept	7.62	0.51	6.54, 8.70	<.0001				
age	**-0.35**	**0.15**	**-0.67, -0.03**	**.033**				
rand. Elo	0.001	0.0005	-0.0003, 0.002	.184				
relative change in coat condition:								
full DRS_{CV}*:*					164.74	0	0.447	30.71 %
Intercept	19.67	14.78	-11.82, 51.17	.203				
DRS_{CV}	-13.39	7.44	-29.76, 1.97	.082				
age	8.92	4.48	-0.63, 18.48	.065				
rand. Elo	-0.02	0.01	-0.05, 0.004	.088				
full DRS:					166.92	2.18	0.150	23.35 %
Intercept	11.91	15.18	-20.44, 44.26	.445				
DRS	-0.01	0.01	-0.03, 0.01	.243				
age	7.21	4.56	-2.51, 16.93	.135				
rand. Elo	-0.02	0.01	-0.05, 0.01	.146				
null model:					164.95	0.21	0.403	17.78 %
Intercept	12.81	15.38	-19.80, 45.42	.417				
age	5.95	4.50	-3.60, 15.5	.205				
rand. Elo	-0.02	0.01	-0.05, 0.01	.112				
mean delta coat temperature:								
full DRS_{CV}*:*					69.67	0.58	0.391	20.58 %
Intercept	-6.53	2.30	-11.59, -1.46	.016				
DRS_{CV}	2.40	1.3	-0.45, 5.26	.091				
age	-0.03	0.55	-1.23, 1.18	.964				
rand. Elo	0.0004	0.002	-0.004, 0.004	.840				
full DRS:					72.68	3.59	0.087	6.46 %
Intercept	-5.67	2.60	-11.39, 0.06	.052				
DRS	0.003	0.003	-0.004, 0.01	.386				
age	0.25	0.59	-1.05, 1.55	.679				
rand. Elo	0.00005	0.002	-0.004, 0.004	.981				
null model:					69.09	0	0.523	1.09 %
Intercept	-4.44	2.20	-9.24, 0.36	.067				
age	0.22	0.58	-1.05, 1.5	.712				
rand. Elo	-0.0003	0.002	-0.005, 0.004	.887				

Appendix V – II Demographic factors

Table A V-II 1 Details on the full and null LMs regarding males' R_{coat}, using rank category and mean randomised Elo-rating as predictors. Models included age.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	$\Delta\ \text{AIC}_C$	**ω**	Marginal R^2
full model:					15.52	3.19	0.142	26.19%
Intercept	0.47	0.27	-0.14, 1.09	.114				
rank category	-0.15	0.12	-0.43, 0.12	.237				
age	-0.06	0.1	-0.28, 0.16	.542				
full model:					15.37	3.04	0.154	27.05%
Intercept	-0.29	0.47	-1.36, 0.79	.556				
rand. Elo	0.0004	0.0003	-0.0003, 0.001	.220				
age	-0.07	0.09	-0.28, 0.14	.465				
null model:					12.33	0	0.704	15.18%
Intercept	0.27	0.22	-0.23, 0.79	.256				
age	-0.12	0.09	-0.31, 0.08	.214				

Table A V-II 2 Details on the full and null LMs regarding males' R_{change}, using rank category and mean randomised Elo-rating as predictors. Models included age.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2
full model:					90.24	4.59	0.084	10.38%
Intercept	-8.08	7.97	-26.46, 10.29	.340				
rank category	2.52	3.59	-5.77, 10.8	.504				
age	1.14	2.84	-5.42, 7.70	.699				
full model:					90.09	4.44	0.090	11.38%
Intercept	4.97	13.89	-27.05, 36.99	.730				
rand. Elo	-0.01	0.01	-0.03, 0.02	.458				
age	1.24	2.72	-5.03, 7.51	.661				
null model:					85.65	0	0.826	6.61%
Intercept	-4.69	6.14	-18.57, 9.2	.465				
age	2.06	2.45	-3.48, 7.60	.422				

Table A V-II 3 Details on the full and null LMs regarding males' R_{temp}, using rank category and mean randomised Elo-rating as predictors. Models included age.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2
full model:					46.07	4.69	0.082	6.07%
Intercept	0.04	1.07	-2.43, 2.51	.970				
rank category	-0.31	0.48	-1.42, 0.80	.541				
age	0.28	0.38	-0.60, 1.16	.488				
full model:					46.54	5.16	0.065	2.75%
Intercept	-0.78	1.92	-5.2, 3.65	.696				
rand. Elo	0.0003	0.001	-0.003, 0.004	.820				
age	0.2	0.38	-0.67, 1.07	.610				
null model:					41.38	0	0.854	2.47%
Intercept	-0.37	0.82	-2.23, 1.48	.658				
age	0.16	0.33	-0.58, 0.91	.627				

Table A V-II 4 Details on the full and null LMs regarding females' R_{coat}, using rank category and mean randomised Elo-rating as predictors. Models included age.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2
full model:					35.25	1.21	0.255	27.11%
Intercept	1.16	0.51	0.09, 2.24	.036				
rank category	-0.19	0.14	-0.49, 0.11	.196				
age	**-0.35**	**0.15**	**-0.67, -0.04**	**.03**				
full model:					35.08	1.04	0.278	27.72%
Intercept	0.04	0.50	-1.03, 1.11	.943				
rand. Elo	0.001	0.0004	-0.0003, 0.002	.178				
age	**-0.36**	**0.15**	**-0.67, -0.05**	**.027**				
null model:					34.04	0	0.466	20.52%
Intercept	0.61	0.31	-0.04, 1.26	.063				
age	**-0.32**	**0.15**	**-0.64, -0.01**	**.046**				

Table A V-II 5 Details on the full and null LMs regarding females' R_{change}, using rank category and mean randomised Elo-rating as predictors. Models included age.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2
full model:					161.61	0.14	0.342	24.69%
Intercept	-33.11	14.12	-63.04, -3.18	.032				
rank category	7.21	3.97	-1.19, 15.62	.088				
age	7.66	4.10	-1.04, 16.36	.081				
full model:					161.47	0	0.366	25.18%
Intercept	8.65	14.04	-21.12, 38.41	.547				
rand. Elo	-0.02	0.01	-0.05, 0.003	.082				
age	7.92	4.11	-0.8, 16.63	.072				
null model:					161.92	0.45	0.292	11.25%
Intercept	-12.38	8.87	-31.1, 6.34	.181				
age	6.53	4.32	-2.59, 15.66	.149				

Table A V-II 6 Details on the full and null LMs regarding females' R_{temp}, using rank category and mean randomised Elo-rating as predictors. Models included age.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	ΔAIC_C	ω	Marginal R^2
full model:					65.01	3.77	0.116	0.27%
Intercept	-0.29	1.89	-4.42, 3.83	.879				
rank category	0.11	0.58	-1.15, 1.37	.849				
age	0.001	0.51	-1.11, 1.11	.998				
full model:					65.00	3.76	0.117	0.32%
Intercept	-0.33	1.92	-4.52, 3.86	.868				
rand. Elo	0.0004	0.002	-0.003, 0.004	.837				
age	-0.02	0.51	-1.13, 1.09	.970				
null model:					61.24	0	0.767	0.002%
Intercept	0.01	0.99	-2.13, 2.16	.988				
age	-0.01	0.49	-1.06, 1.05	.988				

Appendix V – III Reproduction and mean physiological stress response levels

Table A V-III 1 Details on the full and null LM regarding males' R_{coat}, using mean fGCM concentration as predictor in the full model. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	ΔAIC_C	ω	Marginal R^2
full model:					22.59	7.07	0.028	25.10%
Intercept	0.83	0.91	-1.31, 2.98	.390				
mean fGCM	-0.001	0.0004	-0.001, 0.001	.691				
age	-0.06	0.10	-0.30, 0.18	.558				
rank category	-0.18	0.14	-0.52, 0.16	.245				
null model:					15.52	0	0.972	26.19%
Intercept	0.47	0.27	-0.14, 1.09	.114				
age	-0.06	0.1	-0.28, 0.16	.542				
rank category	-0.15	0.12	-0.43, 0.12	.237				

Table A V-III 2 Details on the full and null LM regarding males' R_{change}, using mean fGCM concentration as predictor in the full model. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	ΔAIC_C	ω	Marginal R^2
full model:					97.57	7.33	0.025	9.22%
Intercept	-6.86	27.41	-71.68, 57.95	.810				
mean fGCM	-0.001	0.01	-0.03, 0.03	.964				
age	1.14	3.04	-6.06, 8.33	.719				
rank category	2.43	4.29	-7.71, 12.56	.589				
null model:					90.24	0	0.975	10.38%
Intercept	-8.08	7.97	-26.46, 10.29	.340				
age	1.14	2.84	-5.42, 7.70	.699				
rank category	2.52	3.59	-5.77, 10.8	.504				

Table A V-III 3 Details on the full and null LM regarding males' R_{temp}, using mean fGCM concentration as predictor in the full model. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	ΔAIC_C	ω	Marginal R^2
full model:					53.26	7.19	0.027	6.17%
Intercept	1.06	3.66	-7.59, 9.71	.780				
mean fGCM	-0.0004	0.001	-0.004, 0.003	.778				
age	0.27	0.41	-0.69, 1.23	.521				
rank category	-0.38	0.57	-1.74, 0.97	.525				
null model:					46.07	0	0.973	6.07%
Intercept	0.04	1.07	-2.43, 2.51	.970				
age	0.28	0.38	-0.60, 1.16	.488				
rank category	-0.31	0.48	-1.42, 0.80	.541				

Table A V-III 4 Details on the full and null LM regarding females' R_{coat}, using mean fGCM concentration as predictor in the full model. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	**ω**	Marginal R^2
full model:					38.63	3.38	0.155	27.12%
Intercept	1.85	1.36	-1.05, 4.76	.195				
mean fGCM	-0.0002	0.0004	-0.001, 0.001	.594				
age	**-0.39**	**0.16**	**-0.73, -0.04**	**.032**				
rank category	-0.25	0.18	-0.65, 0.14	.188				
null model:					35.25	0	0.845	27.11%
Intercept	1.16	0.51	0.09, 2.24	.036				
age	**-0.35**	**0.15**	**-0.67, -0.04**	**.03**				
rank category	-0.19	0.14	-0.49, 0.11	.196				

Table A V-III 5 Details on the full and null LM regarding females' R_{change}, using mean fGCM concentration as predictor in the full model. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	**ω**	Marginal R^2
full model:					165.36	3.75	0.133	23.54%
Intercept	-36.40	38.28	-117.99, 45.18	.357				
mean fGCM	0.001	0.01	-0.02, 0.03	.927				
age	7.82	4.59	-1.96, 17.60	.109				
rank category	7.50	5.16	-3.5, 18.50	.167				
null model:					161.61	0	0.867	24.69%
Intercept	-33.11	14.12	-63.04, -3.18	.032				
age	7.66	4.10	-1.04, 16.36	.081				
rank category	7.21	3.97	-1.19, 15.62	.088				

Table A V-III 6 Details on the full and null LM regarding females' R_{temp}, using mean fGCM concentration as predictor in the full model. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	**ω**	Marginal R^2
full model:					66.76	1.75	0.295	14.68%
Intercept	6.06	4.50	-3.85, 15.97	.205				
mean fGCM	-0.002	0.001	-0.01, 0.001	.152				
age	-0.37	0.54	-1.56, 0.82	.508				
rank category	-0.46	0.66	-1.92, 1	.503				
null model:					65.01	0	0.705	0.27%
Intercept	-0.29	1.89	-4.42, 3.83	.879				
age	-0.001	0.51	-1.11, 1.11	.998				
rank category	0.11	0.58	-1.15, 1.37	.849				

Table A V-III 7 Details on the full and null LMs regarding females' R_{coat}, using the number of surviving infants in the last three years and whether they were lactating during the study period (yes/no factor, with no as reference category) as predictor. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	**ω**	Marginal R^2
full surviving infants:					31.75	0	0.828	47.34%
Intercept	0.07	0.6	-1.21, 1.35	.908				
no. of surviving infants	**0.56**	**0.21**	**0.11, 1.03**	**.019**				
age	-0.23	0.13	-0.52, 0.05	.105				
rank category	-0.07	0.13	-0.34, 0.21	.620				
full lactating:					38.48	6.73	0.029	27.65%
Intercept	1.01	0.57	-0.19, 2.22	.093				
lactating (yes)	0.19	0.29	-0.43, 0.80	.525				
age	**-0.35**	**0.15**	**-0.67, -0.02**	**.036**				
rank category	-0.2	0.15	-0.51, 0.11	.197				
null model:					35.25	3.5	0.144	27.11%
Intercept	1.16	0.51	0.09 2.24	.036				
age	**-0.35**	**0.15**	**-0.67, -0.04**	**.03**				
rank category	-0.19	0.14	-0.49, 0.11	.196				

Table A V-III 8 Details on the full and null LMs regarding females' R_{change}, using the number of surviving infants in the last three years and whether they were lactating during the study period (yes/no factor, with no as reference category) as predictor. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	ω	Marginal R^2
full surviving infants:					163.12	1.51	0.285	31.07%
Intercept	-15.08	19.01	-55.59, 25.43	.440				
no. of surviving infants	-9.36	6.82	-23.89, 5.17	.190				
age	5.66	4.25	-3.40, 14.73	.203				
rank category	5.13	4.15	-3.71, 13.97	.236				
full lactating: *					165.07	3.46	0.108	24.54%
Intercept	-29.98	15.84	-63.73, 3.77	.078	(139.05)	(0.25)		(30.66%)
Lactating (yes)	-3.92	8.06	-21.09, 13.26	.634				
age	7.53	4.21	-1.45, 16.51	.094				
rank category	7.29	4.07	-1.38, 15.96	.093				
null model:					161.61	0	0.607	24.69%
Intercept	-33.11	14.12	-63.04, -3.18	.032	(138.80)	(0)		(18.28%)
age	7.66	4.10	-1.04, 16.36	.081				
rank category	7.21	3.97	-1.19, 15.62	.088				

*** rip influential data point** (AIC_C and effect sizes of model without influential data point in brackets)

Table A V-III 9 Details on the full and null LM regarding females' R_{change} after the influential data point marked in Table A V-III 8 was removed, using whether they were lactating during the study period (yes/no factor, with no as reference category) as predictor. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	Marginal R^2
full lactating:					139.05	0.25	30.66%
Intercept	-26.06	9.58	-46.6, -5.52	.017			
lactating (yes)	9.83	5.53	-2.02, 21.69	.097			
age	2.25	2.74	-3.62, 8.11	.425			
rank category	4.29	2.52	-1.11, 9.69	.111			
null model:					138.80	0	18.28%
Intercept	-10.62	9.71	-41.32, 0.07	.051			
age	2.86	2.90	-3.33, 9.04	.341			
rank category	4.93	2.67	-0.75, 10.61	.084			

Table A V-III 10 Details on the full and null LMs regarding females' R_{temp}, using the number of surviving infants in the last three years and whether they were lactating during the study period (yes/no factor, with no as reference category) as predictor. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	ω	Marginal R^2
full surviving infants: *					65.73	0.72	0.331	19.34%
Intercept	2.21	2.21	-2.66, 7.08	.340	(52.50)^1	(4.83)^1		(4.92%)^1
no. of surviving infants	-1.50	0.83	-3.32, 0.32	.096				
age	-0.37	0.51	-1.48, 0.75	.488				
rank category	-0.09	0.54	-1.27, 1.10	.878				
full lactating: **					66.78	1.77	0.195	14.55%
Intercept	-2.36	2.25	-7.30, 2.59	.316	(44.55)^2	(4.46)^2		(31.87%)^2
lactating (yes)	1.56	1.02	-0.68, 3.79	.154				
age	0.09	0.49	-0.98, 1.16	.863				
rank category	0.37	0.57	-0.89, 1.63	.535				
null model:					65.01	0	0.474	0.27%
Intercept	-0.29	1.89	-4.42, 3.83	.879	(47.67)^1	(0)^1		(4.08%)^1
age	0.001	0.51	-1.11, 1.11	.998	(40.09)^2	(0)^2		(29.01%)^2
rank category	0.11	0.58	-1.15, 1.37	.849				

*** mel influential data point; ** mel and gru influential data points** (AIC_C and effect sizes of models without influential data point in brackets and superscript numbers mark comparable models)

Table A V-III 11 Details on the full and null LMs regarding females' R_{temp} after the influential data points marked in Table A V-III 10 were removed, using the number of surviving infants in the last three years and whether they were lactating during the study period (yes/no factor, with no as reference category) as predictor. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	Marginal R^2
full surviving infants:					52.50	4.83	4.92%
Intercept	0.51	1.6	-3.04, 4.07	.755			
no. of surviving infants	0.31	0.76	-1.38, 1.99	.695			
age	0.11	0.37	-0.72 0.95	.769			
rank category	-0.25	0.37	-1.08, 0.59	.522			
null model:					47.67	0	4.08%
Intercept	0.92	1.18	-1.67, 3.52	.450			
age	0.04	0.31	-0.64, 0.72	.910			
rank category	-0.26	0.36	-1.05, 0.53	.485			
full lactating:					44.55	4.46	31.87%
Intercept	0.52	1.57	-3.04, 4.08	.750			
lactating (yes)	0.81	0.90	-1.23, 2.86	.393			
age	0.32	0.29	-0.32, 0.97	.289			
rank category	-0.66	0.35	-1.46, 0.14	.095			
null model:					40.09	0	29.01%
Intercept	1.60	1	-0.61, 3.82	.138			
age	0.23	0.26	-0.36, 0.81	.407			
rank category	-0.72	0.34	-1.48, 0.04	.062			

Table A V-III 12 Details on the full and null LMs regarding females' R_{coat}, using the factor of whether they lost an infant in the last three years (yes/no factor, with no as reference category) as predictor. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	**ω**	Marginal R^2
full lost infant:					35.80	0.55	0.432	36.15%
Intercept	1.21	0.48	0.18, 2.23	.025				
lost infant (yes)	-0.42	0.25	-0.95, 0.12	.118				
age	**-0.36**	**0.14**	**-0.66, -0.06**	**.021**				
rank category	-0.16	0.14	-0.45, 0.13	.268				
null model:					35.25	0	0.568	27.11%
Intercept	1.16	0.51	0.09 2.24	.036				
age	**-0.35**	**0.15**	**-0.67, -0.04**	**.03**				
rank category	-0.19	0.14	-0.49, 0.11	.196				

Table A V-III 13 Details on the full and null LMs regarding females' R_{change}, using the factor of whether they lost an infant in the last three years (yes/no factor, with no as reference category) as predictor. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	**ω**	Marginal R^2
full lost infant:					165.01	3.4	0.155	24.76%
Intercept	-33.51	14.46	-64.33, -2.69	.035				
lost infant (yes)	4.03	7.53	-12.02, 20.09	.600				
age	7.77	4.20	-1.19, 16.73	.084				
rank category	6.87	4.11	-1.88, 15.62	.115				
null model:					161.61	0	0.845	24.69%
Intercept	-33.11	14.12	-63.04, -3.18	.032				
age	7.66	4.10	-1.04, 16.36	.081				
rank category	7.21	3.97	-1.19, 15.62	.088				

Table A V-III 14 Details on the full and null LMs regarding females' R_{temp}, using the factor of whether they lost an infant in the last three years (yes/no factor, with no as reference category) as predictor. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	**ω**	Marginal R^2
full lost infant:					69.63	4.61	0.09	0.48%
Intercept	-0.31	1.98	-4.66, 4.04	.889				
lost infant (yes)	-0.18	0.98	-2.33, 1.98	.859				
age	0.01	0.54	-1.17, 1.19	.982				
rank category	0.13	0.61	-1.21, 1.46	.838				

null model:					65.01	0	0.91	0.27%
Intercept	-0.29	1.89	-4.42, 3.83	.879				
age	0.001	0.51	-1.11, 1.11	.998				
rank category	0.11	0.58	-1.15, 1.37	.849				

Appendix V – IV Social and behavioural mediation

BEHAVIOUR

Table A V-IV 1 Details on the full and null LMs regarding males' R_{coat}, using overall behavioural rates (i.e. scratching, all self-directed behaviour, giving grooming, receiving grooming, aggression, and agonism) as predictor. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	ω	Marginal R^2
full scratching:					21.65	6.13	0.029	29.95%
Intercept	1.16	0.80	-0.74, 3.06	.194				
scratching/hour	-0.03	0.03	-0.09, 0.04	.398				
age	-0.1	0.10	-0.34, 0.15	.387				
rank category	-0.14	0.12	-0.43, 0.15	.297				
full SDB:					20.24	4.72	0.059	36.79%
Intercept	1.28	0.64	-0.24, 2.80	.086				
SDB/hour	-0.03	0.02	-0.08, 0.02	.213				
age	-0.12	0.1	-0.35, 0.12	.282				
rank category	-0.09	0.12	-0.38, 0.2	.475				
full giv. grooming:					17.54	2.02	0.229	13.9%
Intercept	0.28	0.26	-0.31, 0.87	.303				
grooming/hour	-1.24	8.83	-21.6, 19.12	.892				
age	-0.12	0.09	-0.33, 0.1	.247				
full rec. grooming:					22.53	7.01	0.019	25.43%
Intercept	0.40	0.32	-0.35, 1.16	.248				
grooming/hour	1.37	2.98	-5.67, 8.41	.659				
age	-0.06	0.10	-0.30, 0.17	.542				
rank category	-0.16	0.13	-0.46, 0.14	.258				
full aggression:					22.56	7.04	0.019	25.28%
Intercept	0.66	0.52	-0.56, 1.88	.239				
aggression/hour	-0.03	0.06	-0.16, 0.11	.673				
age	-0.07	0.10	-0.32, 0.17	.507				
rank category	-0.17	0.13	-0.48, 0.14	.240				
full agonism:					22.85	7.33	0.016	23.73%
Intercept	0.51	0.62	-0.96, 1.98	.437				
agonism/hour	-0.01	0.07	-0.17, 0.16	.945				
age	-0.06	0.10	-0.31, 0.18	.568				
rank category	-0.16	0.13	-0.47, 0.16	.279				
null model:					15.52	0	0.628	26.19%
Intercept	0.47	0.27	-0.14, 1.09	.114				
age	-0.06	0.1	-0.28, 0.16	.542				
rank category	-0.15	0.12	-0.43, 0.12	.237				

Table A V-IV 2 Details on the full and null LMs regarding males' R_{change}, using overall behavioural rates (i.e. scratching, all self-directed behaviour, giving grooming, receiving grooming, aggression, and agonism) as predictor. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	ω	Marginal R^2
full scratching:					97.57	8.04	0.010	9.21%
Intercept	-7.16	25.33	-67.07, 52.74	.786				
scratching/hour	-0.03	0.90	-2.17, 2.10	.970				
age	1.09	3.28	-6.67, 8.86	.749				
rank category	2.54	3.88	-6.63, 11.70	.534				

full SDB:					97.55	8.02	0.010	9.33%
Intercept	-10.42	21.59	-61.47, 40.64	.644				
SDB/hour	0.08	0.68	-1.54, 1.7	.910				
age	1.3	3.32	-6.55, 9.14	.707				
rank category	2.34	4.12	-7.40, 12.08	.588				
full giv. grooming:					89.53	0	0.548	15.03%
Intercept	-7.57	6.73	-23.09, 7.95	.293				
grooming/hour	239.36	232.82	-297.51, 776.23	.334				
age	1.88	2.45	-3.77, 7.53	.465				
full rec. grooming:					97.54	8.01	0.010	9.41%
Intercept	-7.39	9.67	-30.27, 15.48	.470				
grooming/hour	-13.48	90.11	-226.55, 199.59	.885				
age	1.18	3.05	-6.02, 8.38	.710				
rank category	2.54	3.84	-6.54, 11.62	.529				
full aggression:					97.14	7.61	0.012	11.76%
Intercept	-14.86	15.30	-51.05, 21.33	.364				
aggression/hour	0.92	1.75	-3.21, 5.05	.614				
age	1.58	3.09	-5.74, 8.9	.626				
rank category	3.06	3.90	-6.17, 12.29	.459				
full agonism:					95.65	6.12	0.026	20.25%
Intercept	-25.57	17.03	-65.85, 14.71	.177				
agonism/hour	2.21	1.92	-2.32, 6.74	.286				
age	1.74	2.84	-4.96, 8.44	.559				
rank category	3.59	3.64	-5.02, 12.20	.357				
null model:					90.24	0.71	0.384	10.38%
Intercept	-8.08	7.97	-26.46, 10.29	.340				
age	1.14	2.84	-5.42, 7.70	.699				
rank category	2.52	3.59	-5.77, 10.8	.504				

Table A V-IV 3 Details on the full and null LMs regarding males' R_{temp}, using overall behavioural rates (i.e. scratching, all self-directed behaviour, giving grooming, receiving grooming, aggression, and agonism) as predictor. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	**ω**	Marginal R^2
full scratching:					43.81	0.95	0.311	52.59%
Intercept	-6.42	2.2	-11.63, -1.22	.022	(38.46)	(0)		(45.22%)
scratching/hour	**0.25**	**0.08**	**0.06, 0.43**	**.017**				
age	0.61	0.29	-0.06, 1.29	.069				
rank category	-0.45	0.34	-1.25, 0.34	.22				
full SDB:					42.86	0	0.501	55.99%
Intercept	-5.5	1.8	-9.75, -1.25	.018	(44.91)	(6.45)		(52.53%)
SDB/hour	**0.19**	**0.06**	**0.06, 0.33**	**.012**				
age	0.65	0.28	-0.003, 1.30	.051				
rank category	-0.73	0.34	-1.54, 0.08	.072				
full giv. grooming: *****					46.6	3.74	0.077	2.33%
Intercept	-0.42	0.96	-2.62, 1.79	.673	(40.55)	(2.09)		(34.33%)
grooming/hour	3.66	33.08	-72.61, 79.94	.915				
age	0.16	0.35	-0.64, 0.96	.654				
full rec. grooming: *****					52.35	9.49	0.004	11.66%
Intercept	-0.45	1.24	-3.39, 2.48	.726	(44.78)	(6.32)		(6.90%)
grooming/hour	9.66	11.56	-17.67, 36.98	.431				
age	0.25	0.39	-0.67, 1.17	.542				
rank category	-0.33	0.49	-1.49, 0.84	.529				
full aggression: *****					53.11	10.25	0.003	7.14%
Intercept	0.79	2.07	-4.09, 5.68	.712	(45.06)	(6.6)		(4.87%)
aggression/hour	-0.10	0.24	-0.66, 0.46	.677				
age	0.23	0.42	-0.76, 1.22	.601				
rank category	-0.37	0.53	-1.62, 0.88	.507				
full agonism: *****					53.28	10.42	0.003	6.09%
Intercept	0.66	2.48	-5.21, 6.52	.799	(45.23)	(6.77)		(3.59%)
agonism/hour	-0.08	0.28	-0.74, 0.58	.789				
age	0.26	0.41	-0.72, 1.23	.554				
rank category	-0.35	0.53	-1.60, 0.91	.535				

null model:					46.07 (41.26)	3.21 (2.8)	0.101	6.07% (30.28%)
Intercept	0.04	1.07	-2.43, 2.51	.970				
age	0.28	0.38	-0.60, 1.16	.488				
rank category	-0.31	0.48	-1.42, 0.80	.541				

*** nat influential data point** (AIC$_C$ and effect sizes of models without influential data point in brackets)

Table A V-IV 4 Details on the full and null LMs regarding males' R_{temp} after the influential data point marked in Table A V-IV 3 was removed, using overall behavioural rates (i.e. scratching, all self-directed behaviour, giving grooming, receiving grooming, aggression, and agonism) as predictor. Models included age and rank category. Models on scratching and all self-directed behaviours were included for comparability reasons.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2
full scratching:					38.46	0	0.571	45.22%
Intercept	-7.68	2.84	-14.41, -0.95	.031				
scratching/hour	**0.28**	**0.11**	**0.02, 0.54**	**.041**				
age	0.39	0.28	-0.26, 1.05	.200				
full SDB:					44.91	6.45	0.023	52.53%
Intercept	-5.59	2.79	-12.41, 1.23	.092				
SDB/hour	0.19	0.09	-0.04, 0.43	.085				
age	0.64	0.36	-0.23, 1.51	.122				
rank category	-0.72	0.44	-1.79, 0.36	.153				
full giv. grooming:					40.55	2.09	0.201	34.33%
Intercept	-0.81	0.8	-2.69, 1.08	.346				
grooming/hour	-114.34	59.05	-253.96, 25.29	.094				
age	0.83	0.41	-0.14, 1.8	.083				
full rec. grooming:					44.78	6.32	0.024	6.90%
Intercept	-0.88	1.08	-3.43, 1.66	.438				
grooming/hour	3.36	16.46	-35.55, 42.28	.844				
age	0.26	0.43	-0.75, 1.27	.566				
full aggression:					45.06	6.6	0.021	4.87%
Intercept	1.07	1.89	-3.4, 5.54	.589				
aggression/hour	-0.09	0.24	-0.65, 0.47	.715				
rank category	-0.32	0.5	-1.5, 0.85	.534				
full agonism:					45.23	6.77	0.019	3.59%
Intercept	0.81	2.38	-4.82, 6.44	.745				
agonism/hour	-0.04	0.29	-0.72, 0.63	.882				
rank category	-0.29	0.49	-1.45, 0.88	.581				
null model:					41.26	2.8	0.141	30.28%
Intercept	-0.07	0.93	-2.26, 2.12	.943				
age	0.78	0.42	-0.21, 1.78	.106				
rank category	-0.90	0.52	-2.13, 0.33	.126				

Table A V-IV 5 Details on the full and null LMs regarding females' R_{coat}, using overall behavioural rates (i.e. scratching, all self-directed behaviour, giving grooming, receiving grooming, aggression, and agonism) as predictor. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2
full scratching:					33.10	0	0.287	43.81%
Intercept	1.88	0.57	0.77, 3.21	.003				
scratching/hour	**-0.04**	**0.02**	**-0.07, -0.003**	**.034**				
age	**-0.37**	**0.13**	**-0.65, -0.09**	**.012**				
rank category	-0.14	0.13	-0.41, 0.14	.307				
full SDB:					33.76	0.66	0.206	42.02%
Intercept	1.99	0.59	0.73, 3.26	.004				
SDB/hour	**-0.03**	**0.02**	**-0.07, -0.001**	**.045**				
age	**-0.37**	**0.13**	**-0.66, -0.09**	**.014**				
rank category	-0.14	0.13	-0.41, 0.14	.32				
full giv. grooming:					37.86	4.76	0.027	29.69%
Intercept	0.78	0.65	-0.60, 2.16	.249				
grooming/hour	3.63	3.76	-4.38, 11.64	.35				
age	**-0.36**	**0.15**	**-0.68, -0.05**	**.027**				
rank category	-0.16	0.15	-0.47, 0.15	.297				

full rec. grooming:					33.36	0.26	0.252	43.11%
Intercept	0.77	0.48	-0.27, 1.8	.134				
grooming/hour	**6.44**	**2.83**	**0.41, 12.47**	**.038**				
age	**-0.41**	**0.13**	**-0.7, -0.13**	**.008**				
rank category	-0.23	0.13	-0.51, 0.04	.088				
full aggression:					35.97	2.87	0.068	24.52%
Intercept	0.45	0.34	-0.27, 1.17	.203				
aggression/hour	0.08	0.07	-0.07, 0.23	.298				
age	**-0.32**	**0.15**	**-0.63, -0.001**	**.049**				
full agonism:					36.15	3.05	0.062	23.86%
Intercept	0.07	0.62	-1.24, 1.39	.907				
agonism/hour	0.07	0.07	-0.08, 0.23	.333				
age	-0.25	0.17	-0.60, 0.10	.155				
null model:					35.25	2.15	0.098	27.11%
Intercept	1.16	0.51	0.09, 2.24	.036				
age	**-0.35**	**0.15**	**-0.67, -0.04**	**.03**				
rank category	-0.19	0.14	-0.49, 0.11	.196				

Table A V-IV 6 Details on the full and null LMs regarding females' R_{change}, using overall behavioural rates (i.e. scratching, all self-directed behaviour, giving grooming, receiving grooming, aggression, and agonism) as predictor. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	ω	Marginal R^2
full scratching:					164.72	3.7	0.057	25.76%
Intercept	-41.28	18.25	-80.18, -2.38	.039				
scratching/hour	0.37	0.51	-0.72, 1.47	.481				
age	7.87	4.18	-1.04, 16.77	.079				
rank category	6.65	4.10	-2.09, 15.39	.126				
full SDB:					164.69	3.67	0.058	25.85%
Intercept	-41.88	18.62	-81.57, -2.19	.040				
SDB/hour	0.37	0.5	-0.69, 1.42	.473				
age	7.87	4.17	-1.03, 16.76	.079				
rank category	6.60	4.11	-2.16, 15.36	.129				
full giv. grooming:					165.36	4.34	0.042	23.55%
Intercept	-32.02	18.56	-71.58, 7.54	.105				
grooming/hour	-10.23	107.68	-239.74, 219.28	.926				
age	7.7	4.26	-1.37, 16.76	.091				
rank category	7.12	4.22	-1.87, 16.1	.112				
full rec. grooming:					165.35	4.33	0.042	23.56%
Intercept	-32.48	15.62	-65.77, 0.82	.055				
grooming/hour	-10.24	91.23	-204.69, 184.21	.912				
age	7.75	4.32	-1.45, 16.95	.093				
rank category	7.28	4.14	-1.54, 16.09	.099				
full aggression:					161.02	0	0.363	26.78%
Intercept	-4.50	9.12	-23.82, 14.82	.628				
aggression/hour	-3.77	1.91	-7.82, 0.27	.065				
age	6.27	4	-2.21, 14.74	.137				
full agonism:					162.58	1.56	0.167	21.10%
Intercept	10.58	17.24	-25.97, 47.12	.548				
agonism/hour	-3.14	2.05	-7.49, 1.20	.145				
age	3.4	4.64	-6.44, 13.23	.475				
null model:					161.61	0.59	0.271	24.69%
Intercept	-33.11	14.12	-63.04, -3.18	.032				
age	7.66	4.10	-1.04, 16.36	.081				
rank category	7.21	3.97	-1.19, 15.62	.088				

Table A V-IV 7 Details on the full and null LMs regarding females' R_{temp}, using overall behavioural rates (i.e. scratching, all self-directed behaviour, giving grooming, receiving grooming, aggression, and agonism) as predictor. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2
full scratching:					62.77	0.65	0.274	31.68%
Intercept	-2.11	1.73	-5.91, 1.69	.247	(59.78)	(1.42)		(28.95%)
scratching/hour	**0.16**	**0.06**	**0.02, 0.3**	**.028**				
age	-0.05	0.42	-0.98, 0.88	.913				
rank category	-0.70	0.58	-1.97, 0.56	.248				
full SDB:					62.12	0	0.379	34.17%
Intercept	-2.37	1.72	-6.15, 1.42	.197	(59.19)	(0.83)		(31.43%)
SDB/hour	**0.16**	**0.06**	**0.03, 0.30**	**.021**				
age	-0.06	0.41	-0.97, 0.85	.89				
rank category	-0.81	0.58	-2.09, 0.47	.191				
full giv. grooming: *****					69.68	7.56	0.009	0.25%
Intercept	-0.34	2.53	-5.92, 5.24	.896	(61.91)	(3.55)		(19.42%)
grooming/hour	0.38	13.50	-29.34, 30.10	.978				
age	-0.002	0.55	-1.20, 1.20	.997				
rank category	0.12	0.64	-1.29, 1.53	.857				
full rec. grooming:					68.68	6.56	0.014	5.35%
Intercept	-1.07	2.11	-5.72, 3.58	.622				
grooming/hour	9.42	10.84	-14.44, 33.28	.404				
age	-0.06	0.52	-1.20, 1.09	.913				
rank category	0.12	0.58	-1.16, 1.40	.840				
full aggression:					65.02	2.9	0.089	0.21%
Intercept	-0.07	1.15	-2.58, 2.43	.951				
aggression/hour	0.04	0.23	-0.47, 0.55	.867				
age	-0.01	0.51	-1.11, 1.10	.992				
full agonism:					64.03	1.91	0.146	5.74%
Intercept	-1.49	1.91	-5.66, 2.68	.451				
agonism/hour	0.21	0.23	-0.29, 0.71	.374				
age	0.17	0.53	-0.98, 1.32	.750				
null model:					65.01	2.89	0.089	0.27%
Intercept	-0.29	1.89	-4.42, 3.83	.879	(58.36)	(0)		(13.22%)
age	0.001	0.51	-1.11, 1.11	.998				
rank category	0.11	0.58	-1.15, 1.37	.849				

*** nor influential data point** (AIC$_C$ and effect sizes of models without influential data point in brackets)

Table A V-IV 8 Details on the full and null LMs regarding females' R_{temp} after the influential data point marked in Table A V-IV 7 was removed, using overall behavioural rates (i.e. scratching, all self-directed behaviour, and giving grooming) as predictor. Models included age and rank category. Models on scratching and all self-directed behaviours were included for comparability reasons.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	Marginal R^2
full scratching:					59.78	1.42	28.95%
Intercept	-3.03	1.88	-7.23, 1.17	.139			
scratching/hour	0.12	0.07	-0.04, 0.28	.116			
age	-0.03	0.42	-0.96, 0.90	.948			
rank category	-0.05	0.81	-1.85, 1.75	.953			
full SDB:					59.19	0.83	31.43%
Intercept	-3.22	1.86	-7.36, 0.92	.114			
SDB/hour	0.13	0.07	-0.02, 0.28	.090			
age	-0.04	0.41	-0.95, 0.87	.928			
rank category	-0.16	0.81	-1.96, 1.64	.847			
full giv. grooming:					61.91	3.55	19.42%
Intercept	-1.64	2.22	-6.58, 3.29	.475			
grooming/hour	-13.75	12.94	-42.59, 15.08	.313			
age	0.14	0.47	-0.9, 1.18	.765			
rank category	0.89	0.64	-0.53, 2.31	.192			
null model:					58.36	0	13.22%
Intercept	-2.62	2.03	-7.08, 1.85	.224			
age	0.01	0.45	-0.98, 1.01	.974			
rank category	0.9	.064	-0.51, 2.31	.188			

SOCIAL BONDS

Table A V-IV 9 Details on the full and null LMs regarding males' R_{coat}, using measures of bond strength based on dyadic CSIs as predictors (i.e. the sum of the top 3 CSI scores, the highest CSI score, the number of strong bonds with CSI > 1, and the number of weak bonds with CSI < 1). Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	ω	Marginal R^2
full sum (CSI top 3):					17.94	2.42	0.193	46.79%
Intercept	026	0.25	-0.34, 0.86	.340				
sum (top 3 CSI)	0.02	0.01	-0.003, 0.04	.088				
age	-0.06	0.08	-0.25, 0.13	.482				
rank category	-0.18	0.10	-0.42, 0.07	.128				
full highest CSI:					19.88	4.36	0.073	38.43%
Intercept	0.37	0.26	-0.25, 0.98	.200				
highest CSI	0.03	0.02	-0.02, 0.07	.184				
age	-0.08	0.09	-0.3, 0.13	.393				
rank category	-0.18	0.11	-0.45, 0.09	.160				
full no. strong bonds:					20.34	4.82	0.058	36.28%
Intercept	0.18	0.34	-0.62, 0.97	.618				
no. strong bonds	0.05	0.04	-0.04, 0.14	.222				
age	-0.07	0.09	-0.28, 0.15	.483				
rank category	-0.10	0.12	-0.39, 0.18	.420				
full no. weak bonds:					21.70	6.18	0.029	29.68%
Intercept	1.41	1.1	-1.19, 4.01	.240				
no. weak bonds	-0.04	0.04	-0.13, 0.06	.408				
age	-0.06	0.1	-0.29, 0.16	.530				
rank category	-0.12	0.13	-0.42, 0.18	.380				
null model:					15.52	0	0.647	26.19%
Intercept	0.47	0.27	-0.14, 1.09	.114				
age	-0.06	0.1	-0.28, 0.16	.542				
rank category	-0.15	0.12	-0.43, 0.12	.237				

Table A V-IV 10 Details on the full and null LMs regarding males' R_{change}, using measures of bond strength based on dyadic CSIs as predictors (i.e. the sum of the top 3 CSI scores, the highest CSI score, the number of strong bonds with CSI > 1, and the number of weak bonds with CSI < 1). Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	ω	Marginal R^2
full sum (CSI top 3):					97.50	7.26	0.024	9.61%
Intercept	-8.92	9.4	-31.15, 13.3	.374				
sum (top 3 CSI)	0.07	0.34	-0.73, 0.87	.841				
age	1.14	3.03	-6.03, 8.31	.717				
rank category	2.42	3.86	-6.71, 11.54	.551				
full highest CSI:					97.42	7.18	0.025	10.09%
Intercept	-8.83	8.81	-29.66, 11.99	.349				
highest CSI	0.19	0.60	-1.24, 1.61	.767				
age	0.99	3.06	-6.25, 8.23	.756				
rank category	2.34	3.86	-6.79, 11.46	.564				
full no. strong bonds:					97.52	7.28	0.024	9.53%
Intercept	-6.68	11.27	-33.34, 19.97	.572				
no. strong bonds	-0.24	1.29	-3.30, 2.82	.856				
age	1.17	3.04	-6.01, 8.36	.711				
rank category	2.28	4.03	-7.25, 11.81	.590				
full no. weak bonds:					97.20	6.96	0.028	11.41%
Intercept	-24.22	33.99	-104.6, 56.17	.499				
no. weak bonds	0.63	1.28	-2.39, 3.64	.639				
age	1.2	2.99	-5.88, 8.27	.701				
rank category	1.93	3.96	-7.43, 11.3	.640				
null model:					90.24	0	0.900	10.38%
Intercept	-8.08	7.97	-26.46, 10.29	.340				
age	1.14	2.84	-5.42, 7.70	.699				
rank category	2.52	3.59	-5.77, 10.8	.504				

Table A V-IV 11 Details on the full and null LMs regarding males' R_{temp}, using measures of bond strength based on dyadic CSIs as predictors (i.e. the sum of the top 3 CSI scores, the highest CSI score, the number of strong bonds with CSI > 1, and the number of weak bonds with CSI < 1). Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	ΔAIC_C	ω	Marginal R^2
full sum (CSI top 3):					50.07	4	0.094	24.45%
Intercept	0.78	1.09	-1.8, 3.35	.499				
sum (top 3 CSI)	-0.06	0.04	-0.15, 0.03	.160				
age	0.28	0.35	-0.55, 1.11	.456				
rank category	-0.22	0.45	-1.28, 0.83	.634				
*full highest CSI: **					51.86	5.79	0.038	14.54%
Intercept	0.36	1.11	-2.27, 2.98	.757	(49.7)^1	(8.7)^1		(11.57%)^1
highest CSI	-0.08	0.08	-0.26, 0.10	.339				
age	0.34	0.39	-0.57, 1.25	.406				
rank category	-0.23	0.49	-1.38, 0.92	.645				
*full no. strong bonds: ***					49.74	3.67	0.111	26.19%
Intercept	1.45	1.29	-1.59, 4.48	.298	(41.55)^2	(0)^2		(64.08%)^2
no. strong bonds	-0.25	0.15	-0.59, 0.10	.141				
age	0.31	0.35	-0.51, 1.13	.401				
rank category	-0.55	0.46	-1.63, 0.54	.274				
full no. weak bonds:					50.96	4.89	0.060	19.65%
Intercept	-5.27	4.15	-15.09, 4.55	.245				
no. weak bonds	0.21	0.16	-0.16, 0.57	.229				
age	0.3	0.37	-0.57, 1.16	.445				
rank category	-0.50	0.48	-1.64, 0.64	.336				
null model:					46.07	0	0.696	6.07%
Intercept	0.04	1.07	-2.43, 2.51	.970	(41)^1	(0)^1		(11.12%)^1
age	0.28	0.38	-0.60, 1.16	.488	(45.11)^2	(3.56)^2		(3.50%)^2
rank category	-0.31	0.48	-1.42, 0.80	.541				

*** jos influential data point; ** cro influential data point** (AIC_C and effect sizes of models without influential data point in brackets and superscript numbers mark comparable models)

Table A V-IV 12 Details on the full and null LMs regarding males' R_{temp} after the influential data points marked in Table A V-IV 11 were removed, using measures of bond strength based on dyadic CSIs as predictors (i.e. the highest CSI score and the number of strong bonds with CSI > 1). Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	ΔAIC_C	Marginal R^2
full highest CSI:					49.7	8.7	11.57%
Intercept	0.71	1.04	-1.82, 3.25	.517			
highest CSI	0.04	0.10	-0.21, 0.30	.684			
age	-0.17	0.48	-1.34, 1.01	.740			
rank category	-0.45	0.46	-1.58, 0.69	.371			
null model:					41	0	11.12%
Intercept	-0.72	0.97	-1.58, 3.02	.484			
age	-0.05	0.36	-0.91, 0.82	.903			
rank category	-0.39	0.41	-1.36, 0.59	.382			
full no. strong bonds:					41.55	0	64.08%
Intercept	3.69	1.12	0.95, 6.43	.017			
no. strong bonds	**-0.49**	**0.13**	**-0.79, -0.18**	**.008**			
age	-0.05	0.26	-0.69, 0.58	.842			
rank category	-0.63	0.31	-1.38, 0.13	.088			
null model:					45.11	3.56	3.50%
Intercept	0.24	1.18	-2.56, 3.04	.846			
age	0.19	0.44	-0.84, 1.22	.681			
rank category	-0.27	0.51	-1.48, 0.93	.609			

Table A V-IV 13 Details on the full and null LMs regarding females’ R_{coat}, using measures of bond strength based on dyadic CSIs as predictors (i.e. the sum of the top 3 CSI scores, the highest CSI score, the number of strong bonds with CSI > 1, and the number of weak bonds with CSI < 1). Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	**ω**	Marginal R^2
full sum (CSI top 3):					38.90	3.65	0.084	26.22%
Intercept	0.99	0.8	-0.71, 2.69	.235				
sum (top 3 CSI)	0.01	0.02	-0.03, 0.04	.776				
age	**-0.36**	**0.15**	**-0.68, -0.03**	**.034**				
rank category	-0.17	0.17	-0.53, 0.19	.339				
full highest CSI:					38.97	3.72	0.081	25.98%
Intercept	1.25	0.74	-0.33, 2.83	.112				
highest CSI	-0.004	0.03	-0.06, 0.05	.869				
age	**-0.36**	**0.15**	**-0.69, -0.03**	**.036**				
rank category	-0.20	0.16	-0.55, 0.14	.227				
full no. strong bonds:					37.44	2.19	0.173	31.05%
Intercept	0.70	0.65	-0.67, 2.08	.293				
no. strong bonds	0.07	0.06	-0.06, 0.20	.274				
age	**-0.39**	**0.15**	**-0.72, -0.07**	**.02**				
rank category	-0.2	0.14	-0.50, 0.10	.180				
full no. weak bonds:					37.81	2.56	0.144	29.84%
Intercept	2.44	1.39	-0.52, 5.41	.1				
no. weak bonds	-0.05	0.05	-0.15, 0.05	.34				
age	**-0.40**	**0.16**	**-0.74, -0.07**	**.021**				
rank category	-0.21	0.14	-0.52, 0.09	.161				
null model:					35.25	0	0.519	27.11%
Intercept	1.16	0.51	0.09, 2.24	.036				
age	**-0.35**	**0.15**	**-0.67, -0.04**	**.03**				
rank category	-0.19	0.14	-0.49, 0.11	.196				

Table A V-IV 14 Details on the full and null LMs regarding females’ R_{change}, using measures of bond strength based on dyadic CSIs as predictors (i.e. the sum of the top 3 CSI scores, the highest CSI score, the number of strong bonds with CSI > 1, and the number of weak bonds with CSI < 1). Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	**ω**	Marginal R^2
full sum (CSI top 3):					164.86	3.25	0.107	25.26%
Intercept	-22.56	21.99	-69.42, 24.30	.321				
sum (top 3 CSI)	-0.31	0.49	-1.37, 0.74	.535				
age	7.83	4.19	-1.10, 16.77	.081				
rank category	5.72	4.68	-4.25, 15.68	.240				
full highest CSI:					165.37	3.76	0.083	23.51%
Intercept	-32.88	20.64	-76.87, 11.10	.132				
highest CSI	-0.01	0.70	-1.51, 1.48	.988				
age	7.65	4.3	-1.52, 16.81	.096				
rank category	7.18	4.51	-2.43, 16.79	.132				
full no. strong bonds:					164.85	3.24	0.108	25.3%
Intercept	-25.67	18.47	-65.04, 13.70	.185				
no. strong bonds	-1.12	1.75	-4.86, 2.61	.531				
age	8.34	4.32	-0.86, 17.54	.072				
rank category	7.31	4.04	-1.31, 15.93	.091				
full no. weak bonds:					164.11	2.5	0.156	27.80%
Intercept	-69.49	38.63	-151.83, 12.85	.092				
no. weak bonds	1.35	1.33	-1.49, 4.18	.328				
age	9.15	4.36	-0.14, 18.45	.053				
rank category	7.78	4.00	-0.75, 16.31	.071				
null model:					161.61	0	0.546	24.69%
Intercept	-33.11	14.12	-63.04, -3.18	.032				
age	7.66	4.10	-1.04, 16.36	.081				
rank category	7.21	3.97	-1.19, 15.62	.088				

Table A V-IV 15 Details on the full and null LMs regarding females' R_{temp}, using measures of bond strength based on dyadic CSIs as predictors (i.e. the sum of the top 3 CSI scores, the highest CSI score, the number of strong bonds with CSI > 1, and the number of weak bonds with CSI < 1). Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	**ω**	Marginal R^2
full sum (CSI top 3):					68.99	3.98	0.072	3.81%
Intercept	-1.72	2.76	-7.8, 4.37	.547				
sum (top 3 CSI)	0.05	0.07	-0.1, 0.19	.486				
age	-0.03	0.52	-1.18, 1.12	.959				
rank category	0.28	0.64	-1.11, 1.68	.664				
full highest CSI:					69.16	4.15	0.066	2.95%
Intercept	-1.28	2.51	-6.80, 4.24	.619				
highest CSI	0.06	0.09	-0.14, 0.26	.545				
age	0.04	0.53	-1.12, 1.20	.939				
rank category	0.21	0.61	-1.14, 1.57	.735				
full no. strong bonds:					67.07	2.06	0.187	13.20%
Intercept	1.53	2.21	-3.33, 6.39	.507				
no. strong bonds	-0.35	0.24	-0.89, 0.18	.176				
age	0.22	0.51	-0.90, 1.35	.675				
rank category	0.31	0.57	-0.94, 1.56	.596				
full no. weak bonds:					67.46	2.45	0.154	11.38%
Intercept	-7.00	5.38	-18.85, 4.85	.220				
no. weak bonds	0.24	0.18	-0.16, 0.64	.212				
age	0.28	0.54	-0.90, 1.46	.614				
rank category	0.27	0.57	-0.99, 1.53	.643				
null model:					65.01	0	0.522	0.27%
Intercept	-0.29	1.89	-4.42, 3.83	.879				
age	0.001	0.51	-1.11, 1.11	.998				
rank category	0.11	0.58	-1.15, 1.37	.849				

AFFILIATION NETWORK

Table A V-IV 16 Details on the full and null LMs regarding males' R_{coat}, using measures of affiliative network position as predictors (i.e. strength, eigenvector centrality, betweenness centrality, clustering coefficient, and reach). The network was based on dyadic CSI values. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	**ω**	Marginal R^2
full strength:					18.17	2.94	0.091	45.85%
Intercept	0.16	0.28	-0.51, 0.83	.594				
strength	0.01	0.01	-0.003, 0.03	.095				
age	-0.06	0.08	-0.25, 0.14	.515				
rank category	-0.16	0.10	-0.41, 0.08	.162				
full eigenvector centrality:					17.61	2.38	0.120	48.11%
Intercept	0.19	0.26	-0.43, 0.81	.485				
eigenvector cent.	0.68	0.33	-0.1, 1.47	.078				
age	-0.06	0.08	-0.25, 0.13	.457				
rank category	-0.15	0.10	-0.39, 0.09	.189				
full betweenness centrality:					20.83	5.6	0.024	33.97%
Intercept	0.39	0.27	-0.25, 1.03	.196				
betweenness	0.01	0.01	-0.01, 0.04	.273				
age	-0.04	0.09	-0.27, 0.17	.617				
rank category	-0.17	0.12	-0.45, 0.11	.195				
full clustering coefficient:					15.23	0	0.395	22.88%
Intercept	0.25	0.26	-0.39, 0.89	.369				
clustering coef.	0.24	0.333	-0.56, 1.04	.485				
rank category	-0.13	0.1	-0.37, 0.10	.217				

full reach:					20.45	5.22	0.029	35.78%
Intercept	0.10	0.38	-0.8, 1.01	.793				
reach	0.43	0.33	-0.35, 1.22	.232				
age	-0.05	0.09	-0.27, 0.16	.572				
rank category	-0.10	0.12	-0.39, 0.19	.439				
null model:					15.52	0.23	0.341	26.19%
Intercept	0.47	0.27	-0.14, 1.09	.114				
age	-0.06	0.1	-0.28, 0.16	.542				
rank category	-0.15	0.12	-0.43, 0.12	.237				

Table A V-IV 17 Details on the full and null LMs regarding males' R_{change}, using measures of affiliative network position as predictors (i.e. strength, eigenvector centrality, betweenness centrality, clustering coefficient, and reach). The network was based on dyadic CSI values. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	ω	Marginal R^2
full strength:					97.51	16.8	0.000	9.55%
Intercept	-9.24	10.42	-33.87, 15.39	.404				
strength	0.05	0.25	-0.55, 0.65	.853				
age	1.16	3.03	-6.02, 8.33	.714				
rank category	2.48	3.83	-6.58, 11.55	.538				
full eigenvector centrality:					97.57	16.86	0.000	9.20%
Intercept	-8.16	9.94	-31.67, 15.35	.439				
eigenvector cent.	0.19	12.55	-29.48, 29.86	.989				
age	1.14	3.04	-5.05, 8.33	.719				
rank category	2.52	3.84	-6.57, 11.60	.533				
full betweenness centrality:					96.85	16.14	0.000	13.49%
Intercept	-9.68	8.56	-29.91, 10.56	.295				
betweenness	0.22	0.32	-0.53, 0.97	.512				
age	1.36	2.96	-5.64, 8.36	.660				
rank category	2.23	3.74	-6.61, 11.07	.569				
full clustering coefficient:					80.71	0	0.991	4.85%
Intercept	-5.01	9.93	-29.31, 19.29	.632				
clustering coef.	-0.32	12.40	-30.66, 30.02	.980				
rank category	2.35	3.68	-6.66, 11.36	.547				
full reach:					97.57	16.86	0.000	9.20%
Intercept	-8.26	12.69	-38.27, 21.76	.536				
reach	0.20	11.05	-25.94, 26.34	.986				
age	1.15	3.05	-6.06, 8.35	.718				
rank category	2.54	4.07	-7.1, 12.18	.553				
null model:					90.24	9.54	0.008	10.38%
Intercept	-8.08	7.97	-26.46, 10.29	.340				
age	1.14	2.84	-5.42, 7.70	.699				
rank category	2.52	3.59	-5.77, 10.8	.504				

Table A V-IV 18 Details on the full and null LMs regarding males' R_{temp}, using measures of affiliative network position as predictors (i.e. strength, eigenvector centrality, betweenness centrality, clustering coefficient, and reach). The network was based on dyadic CSI values. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	ω	Marginal R^2
full strength:					49.03	8.97	0.010	29.83%
Intercept	1.27	1.15	-1.45, 3.99	.306				
strength	-0.05	0.03	-0.12, 0.01	.107				
age	0.26	0.33	-0.53, 1.05	.461				
rank category	-0.27	0.42	-1.28, 0.73	.538				
full eigenvector centrality:					48.78	8.72	0.012	31.12%
Intercept	1.11	1.08	-1.45, 3.67	.339				
eigenvector cent.	-2.61	1.37	-5.84, 0.62	.097				
age	0.29	0.33	-0.5, 1.07	.414				
rank category	-0.33	0.42	-1.32, 0.66	.454				

full betweenness centrality:					52.24	12.18	0.002	12.31%
Intercept	0.31	1.13	-2.35, 2.97	.791				
betweenness	-0.04	0.04	-0.14, 0.06	.407				
age	0.24	0.39	-0.68, 1.16	.556				
rank category	-0.26	0.49	-1.43, 0.90	.612				
full clustering coefficient: *					40.06 (37.09)^{1}	0 (0)^{1}	0.926	16.81% (48.37%)^{1}
Intercept	1.14	1.04	-1.40, 3.68	.316				
clustering coef.	-0.86	1.3	-4.04, 2.31	.530				
rank category	-0.41	0.39	-1.35, 0.54	.333				
full reach: **					51.53 (41.88)^{2}	11.47 (0)^{2}	0.003	16.44% (63.03%)^{2}
Intercept	1.36	1.57	-2.34, 5.07	.413				
reach	-1.55	1.36	-4.78, 1.67	.292				
age	0.25	0.38	-0.63, 1.14	.520				
rank category	-0.5	0.50	-1.69, 0.69	.353				
null model:					46.07 (45.41)^{1} (45.11)^{2}	6.01 (8.32)^{1} (3.23)^{2}	0.046	6.07% (6.57%)^{1} (3.50%)^{2}
Intercept	0.04	1.07	-2.43, 2.51	.970				
age	0.28	0.38	-0.60, 1.16	.488				
rank category	-0.31	0.48	-1.42, 0.80	.541				

*** dav influential data point; ** cro influential data point** (AIC$_C$ and effect sizes of models without influential data point in brackets and superscript numbers mark comparable models)

Table A V-IV 19 Details on the full and null LMs regarding males' R_{temp} after the influential data points marked in Table A V-IV 18 were removed, using measures of affiliative network position as predictors (i.e. clustering coefficient and reach). The network was based on dyadic CSI values. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	Marginal R^2
full clustering coefficient:					37.09	0	48.37%
Intercept	2.76	1.16	-0.23, 5.75	.064			
clustering coef.	-3.53	1.68	-7.86, 0.8	.090			
rank category	-0.76	0.36	-1.68, 0.16	.087			
null model:					45.41	8.32	6.57%
Intercept	-0.07	1.21	-2.94, 2.81	.959			
age	0.33	0.45	-0.74, 1.40	.493			
rank category	-0.3	0.52	-1.51, 0.92	.584			
full reach:					41.88	0	63.03%
Intercept	55.39	1.52	1.66, 9.11	.012			
reach	**-4.92**	**1.3**	**-8.1, -1.75**	**.009**			
age	-0.33	0.29	-1.04, 0.38	.301			
rank category	-0.71	0.32	-1.49, 0.07	.069			
null model:					45.11	3.23	3.50%
Intercept	0.24	1.18	-2.56, 3.04	.846			
age	0.19	0.44	-0.84, 1.22	.681			
rank category	-0.27	0.51	-1.48, 0.93	.609			

Table A V-IV 20 Details on the full and null LMs regarding females' R_{coat}, using measures of affiliative network position as predictors (i.e. strength, eigenvector centrality, betweenness centrality, clustering coefficient, and reach). The network was based on dyadic CSI values. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	**ω**	Marginal R^2
full strength:					38.81	3.56	0.090	26.55%
Intercept	1.22	0.98	-0.87, 3.31	.234				
strength	0.01	0.01	-0.02, 0.04	.695				
age	**-0.36**	**0.15**	**-0.68, -0.03**	**.033**				
rank category	-0.16	0.17	-0.52, 0.21	.374				

full eigenvector centrality:					38.95	3.7	0.084	26.04%
Intercept	1.61	0.77	-0.04, 3.26	.056				
eigenvector cent.	-0.12	0.58	-1.36, 1.12	.839				
age	**-0.35**	**0.15**	**-0.68, -0.02**	**.04**				
rank category	-0.21	0.16	-0.54, 0.13	.217				
full betweenness centrality:					38.96	3.71	0.084	26.03%
Intercept	1.41	0.83	-0.35, 3.17	.108				
betweenness	0.002	0.01	-0.02, 0.02	.844				
age	**-0.35**	**0.15**	**-0.68, -0.02**	**.039**				
rank category	-0.17	0.17	-0.54, 0.2	.333				
full clustering coefficient:					38.73	3.46	0.094	26.81%
Intercept	1.44	0.65	0.05, 2.83	.044				
clustering coef.	0.48	1.01	-1.68, 2.64	.643				
age	**-0.37**	**0.16**	**-0.71, -0.04**	**.032**				
rank category	-0.19	0.15	-0.51, 0.12	.203				
full reach:					38.38	3.13	0.112	27.99%
Intercept	0.45	1.62	-3.01, 3.91	.785				
reach	1.31	1.84	-2.62, 5.24	.487				
age	**-0.33**	**0.15**	**-0.66, -0.01**	**.046**				
rank category	-0.21	0.15	-0.52, 0.10	.177				
null model:					35.25	0	0.535	27.11%
Intercept	1.52	0.62	0.21, 2.82	.025				
age	**-0.35**	**0.15**	**-0.67, -0.04**	**.03**				
rank category	-0.19	0.14	-0.49, 0.11	.196				

Table A V-IV 21 Details on the full and null LMs regarding females' R_{change}, using measures of affiliative network position as predictors (i.e. strength, eigenvector centrality, betweenness centrality, clustering coefficient, and reach). The network was based on dyadic CSI values. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	$\Delta\ AIC_C$	**ω**	Marginal R^2
full strength:					165.02	6.62	0.027	24.72%
Intercept	-29.81	27.17	-87.72, 28.10	.29				
strength	-0.21	0.39	-1.04, 0.63	.606				
age	7.83	4.21	-1.15, 16.81	.083				
rank category	5.91	4.75	-4.21, 16.03	.232				
full eigenvector centrality:					164.64	6.24	0.033	26.02%
Intercept	-31.48	21.17	-76.60, 12.64	.158				
eigenvector cent.	-12.14	15.88	-45.99, 21.71	.457				
age	8.17	4.21	-0.81, 17.15	.071				
rank category	5.94	4.35	-3.33, 15.21	.192				
full betweenness centrality:					165.23	6.83	0.024	23.98%
Intercept	-35.95	22.90	-84.77, 12.87	.137				
betweenness	-0.08	0.25	-0.61, 0.45	.747				
age	7.47	4.26	-1.61, 16.56	.1				
rank category	6.37	4.82	-4.92, 16.65	.207				
full clustering coefficient:					158.4	0	0.741	44.83%
Intercept	-30.79	15.21	-63.21, 1.62	.061				
clustering coef.	**-60.96**	**23.65**	**-111.36, -10.56**	**.021**				
age	**10.39**	**3.68**	**2.53, 18.24**	**.013**				
rank category	**7.49**	**3.41**	**0.22, 14.76**	**.044**				
full reach:					165.12	6.72	0.026	24.37%
Intercept	-59.37	45.57	-156.49, 27.76	.212				
reach	22.91	51.81	-87.51, 133.33	.665				
age	8.01	4.28	-1.12, 17.14	.081				
rank category	6.95	4.11	-1.81, 15.71	.112				

null model:					161.61	3.21	0.149	24.69%
Intercept	-40.77	17.11	-77.04, -4.51	.03				
age	7.66	4.10	-1.04, 16.36	.081				
rank category	7.21	3.97	-1.19, 15.62	.088				

Table A V-IV 22 Details on the full and null LMs regarding females' R_{temp}, using measures of affiliative network position as predictors (i.e. strength, eigenvector centrality, betweenness centrality, clustering coefficient, and reach). The network was based on dyadic CSI values. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	**ω**	Marginal R^2
full strength:					69.67	4.66	0.055	0.30%
Intercept	-0.49	3.22	-7.58, 6.59	.881				
strength	0.005	0.05	-0.11, 0.12	.930				
age	-0.01	0.54	-1.19, 1.18	.992				
rank category	0.13	0.63	-1.26, 1.52	.842				
full eigenvector centrality:					69.67	4.66	0.055	0.30%
Intercept	-0.4	2.58	-6.07, 5.28	.881				
eigenvector cent.	0.20	2.26	-4.78, 5.19	.930				
age	-0.01	0.54	-1.20, 1.19	.989				
rank category	0.11	0.60	-1.21, 1.44	.852				
full betweenness centrality:					69.59	4.58	0.058	0.73%
Intercept	0.11	2.79	-6.04, 6.26	.969				
betweenness	-0.01	0.03	-0.07, 0.06	.799				
age	-0.01	0.53	-1.18, 1.16	.985				
rank category	0.04	0.66	-1.41, 1.49	.951				
full clustering coefficient:					67.35	2.34	0.176	11.9%
Intercept	-0.9	2.2	-5.74, 3.94	.690				
clustering coef.	4.36	3.20	-2.69, 11.41	.201				
age	-0.18	0.51	-1.3, 0.94	.734				
rank category	0.04	0.56	-1.19, 1.28	.940				
full reach:					68.71	3.7	0.089	5.24%
Intercept	4.35	5.86	-8.55, 17.25	.473				
reach	-6.05	7.05	-21.56, 9.46	.409				
age	-0.06	0.52	-1.21, 1.09	.911				
rank category	0.21	0.6	-1.1, 1.52	.727				
null model:					65.01	0	0.566	0.27%
Intercept	-0.3	2.23	-5.15, 4.56	.897				
age	0.001	0.51	-1.11, 1.11	.998				
rank category	0.11	0.58	-1.15, 1.37	.849				

AFFILIAITON NETWORK – PERMUTATION TESTS

Table A V-IV 23 Details on the permutation procedure regarding the link between males' R_{coat} and their strength in an affiliative network. The network was based on dyadic CSI values, node permutations were repeated 1000 times. Models included age and rank category.

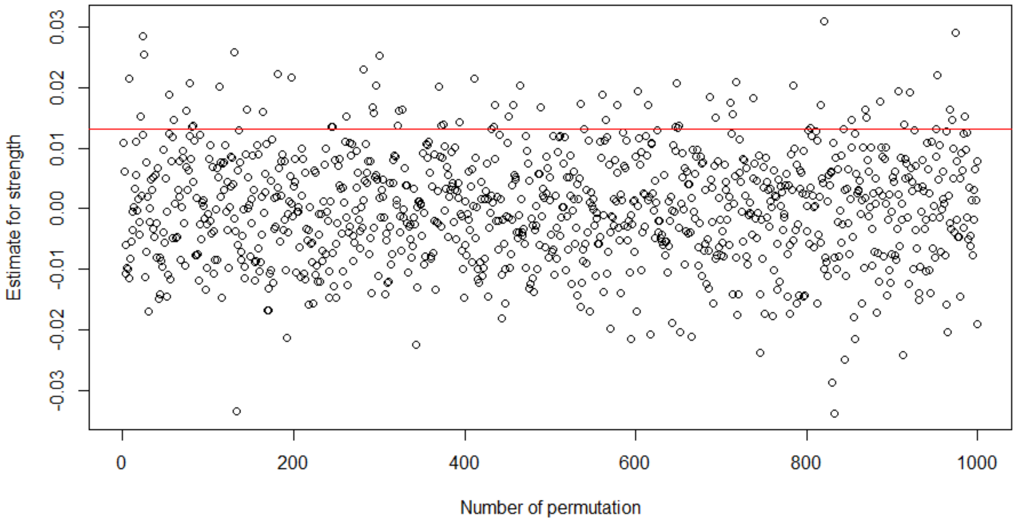
Network metric: strength
Model: R_{coat} ~ strength + age + rank
Proportion observed est. < randomised est.: 0.071


Table A V-IV 24 Details on the permutation procedure regarding the link between males' R_{coat} and their eigenvector centrality in an affiliative network. The network was based on dyadic CSI values, node permutations were repeated 1000 times. Models included age and rank category.

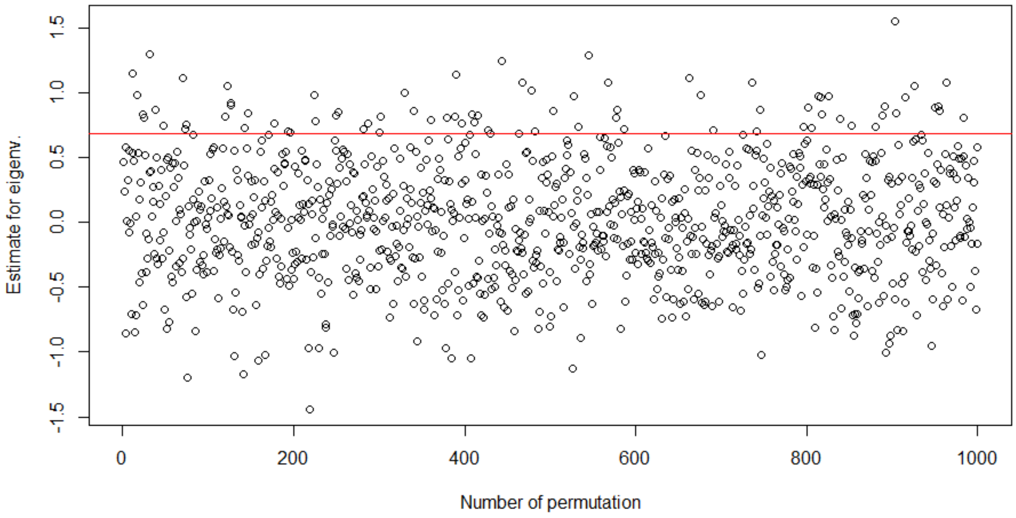
Network metric: eigenvector centrality
Model: R_{coat} ~ eigenvector centrality + age + rank
Proportion observed est. < randomised est.: 0.077


Table A V-IV 25 Details on the permutation procedure regarding the link between males’ R$_{coat}$ and their clustering coefficient in an affiliative network. The network was based on dyadic CSI values, node permutations were repeated 1000 times. Models included rank category, while age was excluded due to VIFs > 2 between age and clustering coefficient.

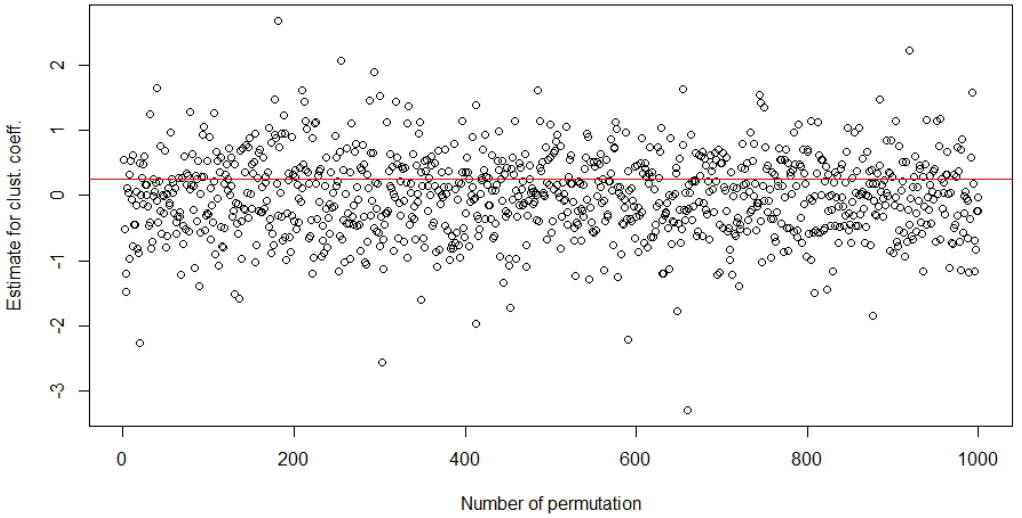
Network metric: individual clustering coefficient
Model: R$_{coat}$ ~ individual clustering coefficient + rank
Proportion observed est. < randomised est.: 0.345


Table A V-IV 26 Details on the permutation procedure regarding the link between males’ R$_{change}$ and their clustering coefficient in an affiliative network. The network was based on dyadic CSI values, node permutations were repeated 1000 times. Models included rank category, while age was excluded due to VIFs > 2 between age and clustering coefficient.

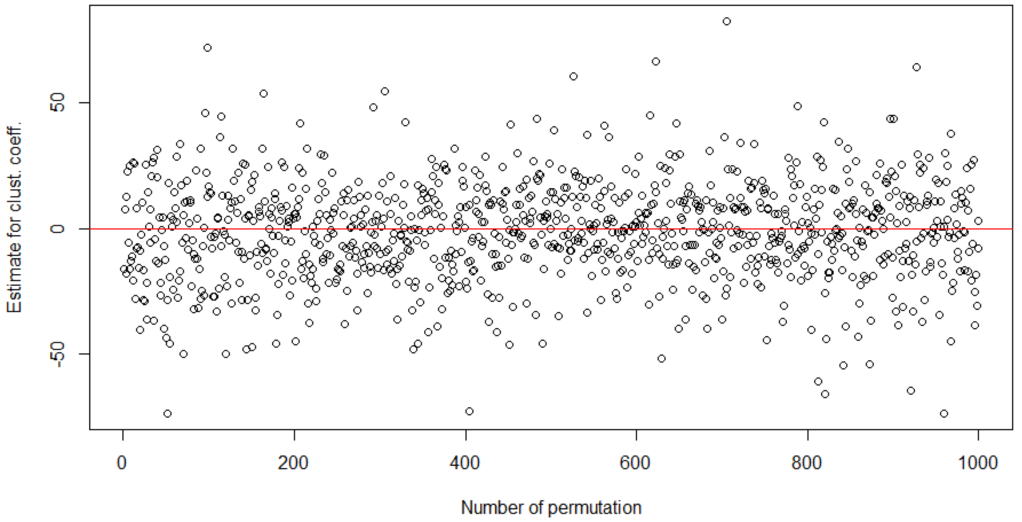
Network metric: individual clustering coefficient
Model: R$_{change}$ ~ individual clustering coefficient + rank
Proportion observed est. < randomised est.: 0.487


Table A V-IV 27 Details on the permutation procedure regarding the link between males' R_{temp} and their clustering coefficient in an affiliative network. The network was based on dyadic CSI values, node permutations were repeated 1000 times. Models included rank category, while age was excluded due to VIFs > 2 between age and clustering coefficient.

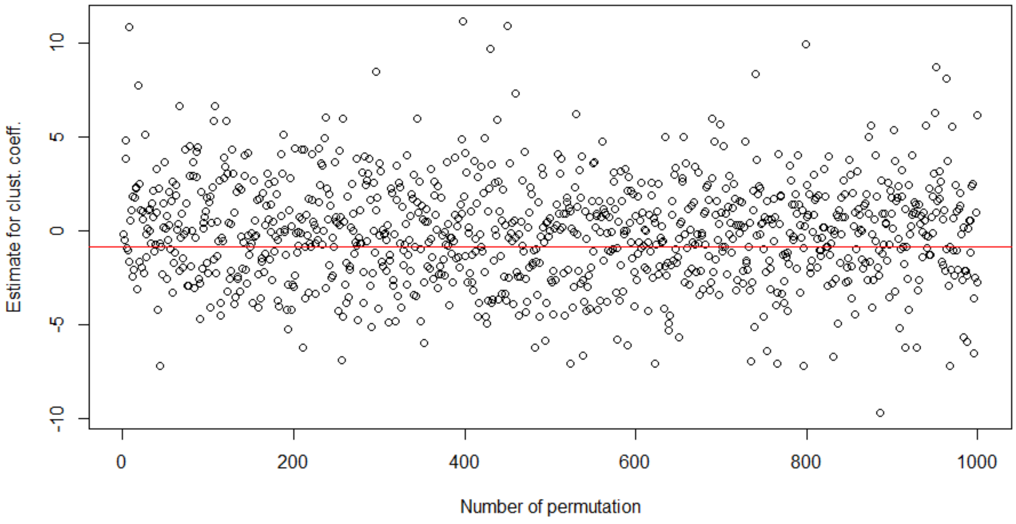
Network metric: individual clustering coefficient
Model: R_{temp} ~ individual clustering coefficient + rank
Proportion observed est. < randomised est.: 0.624


Table A V-IV 28 Details on the permutation procedure regarding the link between males' R_{temp} and their reach in an affiliative network. The network was based on dyadic CSI values, node permutations were repeated 1000 times. Models included age and rank category.

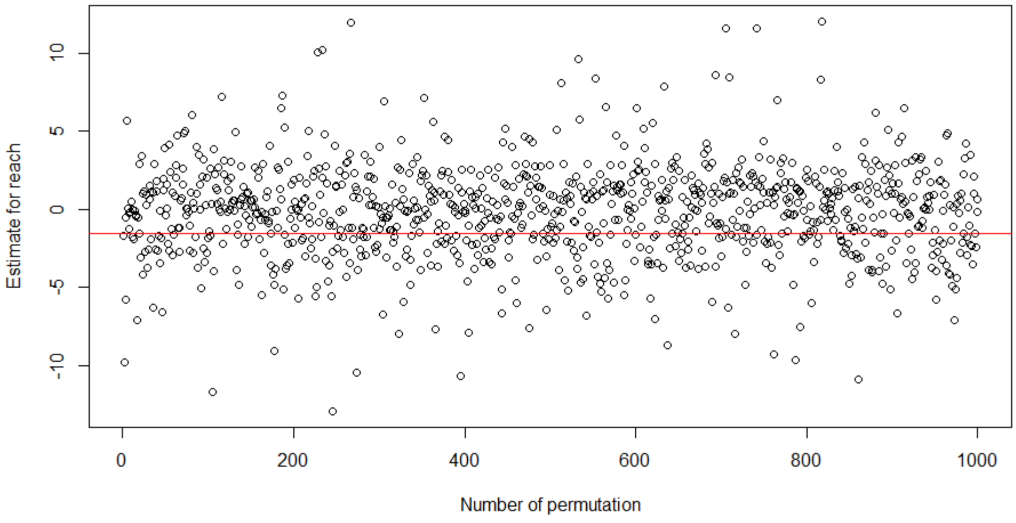
Network metric: reach
Model: R_{temp} ~ reach + age + rank
Proportion observed est. < randomised est.: 0.7


Table A V-IV 29 Details on the permutation procedure regarding the link between females' R_{change} and their clustering coefficient in an affiliative network. The network was based on dyadic CSI values, node permutations were repeated 1000 times. Models included age and rank category.

Network metric: individual clustering coefficient

Model: R_{change} ~ individual clustering coefficient + age + rank

Proportion observed est. < randomised est.: 0.998

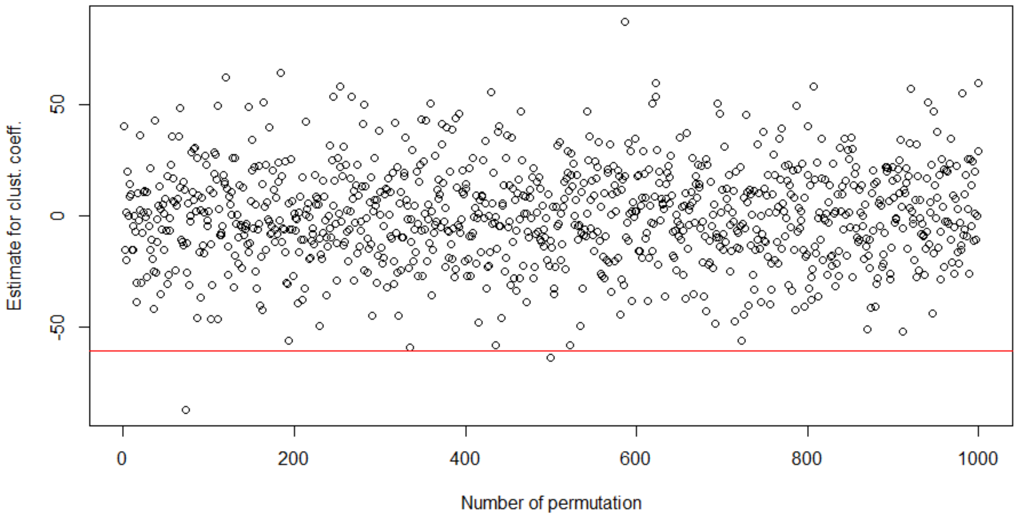
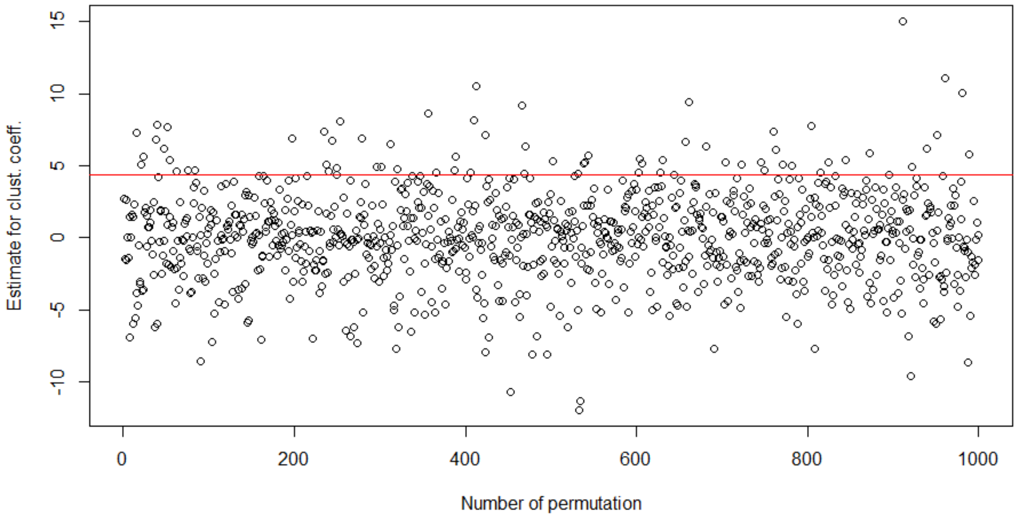


Table A V-IV 30 Details on the permutation procedure regarding the link between females' R_{temp} and their clustering coefficient in an affiliative network. The network was based on dyadic CSI values, node permutations were repeated 1000 times. Models included age and rank category.

Network metric: individual clustering coefficient

Model: R_{temp} ~ individual clustering coefficient + age + rank

Proportion observed est. < randomised est.: 0.07



AGONISM NETWORK

Table A V-IV 31 Details on the full and null LMs regarding males' R_{coat}, using measures of agonistic network position as predictors (i.e. strength, degree, eigenvector centrality, betweenness centrality, clustering coefficient, and reach). The undirected network was based on all agonistic interactions. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	ω	Marginal R^2
*full strength: **					22.53	7.01	0.015	25.44%
Intercept	0.19	0.67	-1.4, 1.78	.784	(21.22)	(7.68)		(22.13%)
strength	0.05	0.12	-0.23, 0.34	.658				
age	-0.06	0.10	-0.29, 0.18	.600				
rank category	-0.12	0.14	-0.46, 0.21	.416				
full degree:					15.84	0.32	0.410	24.32%
Intercept	-0.33	0.56	-1.61, 0.95	.568				
degree	0.03	0.02	-0.03, 0.08	.278				
age	-0.11	0.09	-0.31, 0.08	.223				
*full eigenvector centrality: **					22.52 (21.3)	7 (7.76)	0.015	25.48% (21.70%)
Intercept	0.23	0.59	-1.17, 1.63	.708				
eigenvector cent.	0.25	0.54	-1.02, 1.52	.655				
age	-0.05	0.10	-0.29, 0.19	.615				
rank category	-0.13	0.13	-0.45, 0.18	.354				
full betweenness centrality:					22.73	7.21	0.013	24.38%
Intercept	0.56	0.40	-0.4, 1.51	.210				
betweenness	-0.004	0.01	-0.04, 0.03	.782				
age	-0.07	0.10	-0.31, 0.18	.541				
rank category	-0.17	0.14	-0.49, 0.16	.259				
full clustering coefficient:					20.75	5.05	0.035	34.35%
Intercept	-1.62	1.74	-5.73, 2.5	.384				
clustering coef.	3.3	2.72	-3.13, 9.73	.264				
age	-0.02	0.1	-0.26, 0.20	.796				
rank category	-0.26	0.15	-0.60, 0.09	.118				
*full reach: **					20.99	5.47	0.031	33.23%
Intercept	-0.6	0.98	-2.91, 1.71	.560	(22.34)	(8.8)		(15.54%)
reach	1.23	1.09	-1.34, 3.82	.292				
age	-0.04	0.09	-0.27, 0.18	.664				
rank category	-0.1	0.13	-0.40, 0.20	.468				
null model:					15.52	0	0.481	26.19%
Intercept	0.47	0.27	-0.14, 1.09	.114	(13.54)	(0)		(16.33%)
age	-0.06	0.1	-0.28, 0.16	.542				
rank category	-0.15	0.12	-0.43, 0.12	.237				

*** jos influential data point** (AIC_C and effect sizes of models without influential data point in brackets)

Table A V-IV 32 Details on the full and null LMs regarding males' R_{coat} after the influential data point marked in Table A V-IV 31 was removed, using measures of agonistic network position as predictors (i.e. strength, eigenvector centrality, and reach). The undirected network was based on all agonistic interactions. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	Marginal R^2
full strength:					21.22	7.68	22.13%
Intercept	0.86	0.65	-0.73, 2.45	.234			
strength	-0.12	0.13	-0.44, 0.20	.394			
age	0.04	0.1	-0.2, 0.28	.696			
rank category	-0.19	0.12	-05, 0.11	.168			
full eigenvector centrality:					21.3	7.76	21.70%
Intercept	0.75	0.56	-0.61, 2.12	.226			
eigenvector cent.	-0.53	0.59	-1.98, 0.92	.408			
age	0.03	0.1	-0.2, 0.27	.730			
rank category	-0.17	0.11	-0.45, 0.11	.184			

full reach:					22.34	8.8	15.54%
Intercept	0.77	1.37	-2.57, 4.12	.591			
reach	-0.59	1.69	-4.73, 3.55	.740			
age	0.03	0.10	-0.23, 0.28	.788			
rank category	-0.16	0.13	-0.47, 0.16	.267			
null model:					13.54	0	16.33%
Intercept	0.31	0.25	-0.27, 0.89	.251			
age	0.01	0.09	-0.20, 0.24	.853			
rank category	-0.14	0.10	-0.38, 0.11	.238			

Table A V-IV 33 Details on the full and null LMs regarding males' R_{change}, using measures of agonistic network position as predictors (i.e. strength, degree, eigenvector centrality, betweenness centrality, clustering coefficient, and reach). The undirected network was based on all agonistic interactions. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	**ω**	Marginal R^2
full strength:					97.22	6.98	0.014	11.32%
Intercept	-16.81	20.03	-64.18, 30.55	.429.				
strength	1.7	3.53	-6.66, 10.05	646				
age	1.31	3.01	-5.81, 8.43	.677				
rank category	3.46	4.26	-6.61, 13.53	.444				
full degree:					90.4	0.16	0.438	9.32%
Intercept	4.54	16.46	-33.40, 42.49	.789				
degree	-0.43	0.71	-2.06, 1.2	.560				
age	2.01	2.54	-3.86, 7.87	.453				
full eigenvector centrality:					96.71	6.47	0.019	14.29%
Intercept	-19.55	17.24	-60.31, 21.21	.294				
eigenvector cent.	11.8	15.61	-25.11, 48.71	.474				
age	1.49	2.96	-5.51, 8.48	.631				
rank category	3.49	3.91	-5.76, 12.74	.402				
full betweenness centrality: *					96.11 (77.41)	5.87 (0.19)	0.025	17.71% (9.50%)
Intercept	-16.09	11.32	-42.85, 10.66	.198				
betweenness	0.40	0.40	-0.55, 1.36	.352				
age	1.67	2.9	-5.17, 8.52	.581				
rank category	3.85	3.84	-5.22, 12.93	.349				
full clustering coefficient:					97.57	7.33	0.012	9.23%
Intercept	-4.74	57.15	-139.87, 130.4	.936				
clustering coef.	-5.28	89.23	-216.27, 205.71	.954				
age	1.09	3.18	-6.44, 8.61	.743				
rank category	2.68	4.77	-8.61, 13.97	.592				
full reach:					96.91	6.67	0.017	13.12%
Intercept	11.46	30.8	-61.37, 84.28	.721				
reach	-22.64	34.38	-103.92, 58.64	.531				
age	0.82	2.99	-6.26, 7.89	.792				
rank category	1.5	4.03	-8.04, 11.04	.721				
null model:					90.24 (77.22)	0 (0)	0.474	10.38% (10.86%)
Intercept	-8.08	7.97	-26.46, 10.29	.340				
age	1.14	2.84	-5.24, 7.70	.699				
rank category	2.52	3.59	-5.77, 10.8	.504				

*** blo influential data point** (AIC_C and effect sizes of models without influential data point in brackets)

Table A V-IV 34 Details on the full and null LM regarding males' R$_{change}$ after the influential data point marked in Table A V-IV 33 was removed, using measures of agonistic network position as predictors (i.e. betweenness centrality). The undirected network was based on all agonistic interactions. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	Marginal R^2
full betweenness centrality:					77.41	0.19	9.50%
Intercept	0.12	6.76	-15.85, 16.10	.986			
betweenness	-0.11	0.3	-0.81, 0.59	.714			
age	1.29	1.97	-3.37, 5.95	.533			
null model:					77.22	0	10.86%
Intercept	0.52	6.26	-14.28, 15.32	.936			
age	2.11	2.02	-2.66, 6.89	.330			
rank category	-1.51	2.85	-8.24, 5.22	.612			

Table A V-IV 35 Details on the full and null LMs regarding males' R$_{temp}$, using measures of agonistic network position as predictors (i.e. strength, degree, eigenvector centrality, betweenness centrality, clustering coefficient, and reach). The undirected network was based on all agonistic interactions. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	ω	Marginal R^2
full strength:					51.78	8.53	0.008	14.98%
Intercept	2.47	2.54	-3.54, 8.48	.363				
strength	-0.47	0.45	-1.53, 0.59	.328				
age	0.23	0.38	-0.67, 1.13	.563				
rank category	-0.57	0.54	-1.85, 0.71	.326				
full degree:					44.43	1.18	0.302	16.91%
Intercept	2.12	2.04	-2.58, 6.81	.329				
degree	-0.12	0.09	-0.32, 0.09	.221				
age	0.15	0.31	-0.58, 0.88	.646				
*full eigenvector centrality: **					52.89 (49.05)^1	9.64 (8.05)^1	0.004	8.44% (15.56%)^1
Intercept	1.23	2.35	-4.33, 6.79	.617				
eigenvector cent.	-1.22	2.13	-6.26, 3.81	.583				
age	0.24	0.40	-0.71, 1.2	.568				
rank category	-0.41	0.53	-1.67, 0.85	.468				
*full betweenness centrality: ***					53.24 (45.18)^2	9.99 (3.92)^2	0.004	6.34% (3.07%)^2
Intercept	0.41	1.61	-3.40, 4.22	.806				
betweenness	-0.02	0.06	-0.15, 0.12	.756				
age	0.25	0.41	-0.72, 1.23	.559				
rank category	-0.37	0.55	-1.66, 0.92	.520				
*full clustering coefficient: **					53.4 (41.6)^1	10.15 (0.6)^1	0.003	5.35% (6.75%)^1
Intercept	0.03	768	-18.12, 18.18	.997				
clustering coef.	0.03	11.98	-28.31, 28.36	.998				
age	0.28	0.43	-0.73, 1.29	.536				
rank category	-0.31	0.64	-1.833, 1.21	.644				
full reach:					43.25	0	0.545	54.63%
Intercept	8.47	2.69	2.12, 14.83	.016				
reach	**-9.77**	**3**	**-16.86, -2.68**	**.014**				
age	0.14	0.26	-0.48, 0.75	.614				
rank category	-0.75	0.35	-1.58, 0.09	.072				
null model:					46.07 (41)^1 (41.26)^2	2.82 (0)^1 (0)^2	0.133	6.07% (11.12%)^1 (30.28%)^2
Intercept	0.04	1.07	-2.43, 2.51	.970				
age	0.28	0.38	-0.60, 1.16	.488				
rank category	-0.31	0.48	-1.42, 0.80	.541				

*** jos influential data point; ** nat influential data point** (AIC$_C$ and effect sizes of models without influential data point in brackets and superscript numbers mark comparable models)

Table A V-IV 36 Details on the full and null LMs regarding males' R$_{temp}$ after the influential data points marked in Table A V-IV 35 were removed, using measures of agonistic network position as predictors (i.e. eigenvector centrality, clustering coefficient, and betweenness centrality). The undirected network was based on all agonistic interactions. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	Marginal R^2
full eigenvector centrality:					49.05	8.05	15.56%
Intercept	-0.83	2.24	-6.30, 4.65	.725			
eigenvector cent.	1.83	2.37	-3.97, 7.63	.469			
age	-0.10	0.38	-1.04, 0.83	.794			
rank category	-0.26	0.46	-1.38, 0.85	.588			
full clustering coefficient:					41.6	0.6	6.75%
Intercept	-3.74	6.17	-18.32, 10.85	.564			
clustering coef.	5.96	9.32	-16.06, 27.98	.543			
age	-0.25	0.37	-1.12, 0.62	.521			
null model:					41	0	11.12%
Intercept	0.72	0.97	-1.58, 3.02	.484			
age	-0.05	0.36	-0.91, 0.82	.903			
rank category	-0.39	9.41	-1.36, 0.59	.382			
full betweenness centrality:					45.18	3.92	3.97%
Intercept	0.73	1.48	-2.78, 4.23	.638			
betweenness	-0.01	0.06	-0.15, 0.12	.814			
rank category	-0.31	0.51	-2.53, 0.90	.561			
null model:					41.26	0	30.28%
Intercept	-0.07	0.93	-2.26, 2.12	.943			
age	0.78	0.42	-0.21, 1.78	.106			
rank category	-0.90	0.52	-2.13, 0.33	.126			

Table A V-IV 37 Details on the full and null LMs regarding females' R$_{coat}$, using measures of agonistic network position as predictors (i.e. strength, degree, eigenvector centrality, betweenness centrality, clustering coefficient, and reach). The undirected network was based on all agonistic interactions. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	ω	Marginal R^2
full strength:					37.63	4.85	0.055	30.45%
Intercept	0.4	1.22	-2.19, 2.99	.747				
strength	0.23	0.21	-0.23, 0.68	.305				
age	-0.30	0.15	-0.63, 0.03	.068				
rank category	-0.05	0.2	-0.47, 0.38	.822				
full degree:					38.55	5.77	0.035	27.40%
Intercept	0.72	1.46	-2.39, 3.83	.628				
degree	0.03	0.05	-0.08, 0.14	.555				
age	**-0.34**	**0.15**	**-0.66, -0.01**	**.044**				
rank category	-0.15	0.16	-0.49, 0.18	.346				
full eigenvector centrality:					38.14	5.36	0.043	28.76%
Intercept	0.70	1.15	-1.76, 3.16	.552				
eigenvector cent.	1.00	1.20	-1.56, 3.57	.417				
age	-0.31	0.16	-0.65, 0.03	.07				
rank category	-0.08	0.2	-0.50, 0.34	.694				
full betweenness centrality:					38.84	6.06	0.030	26.44%
Intercept	1.36	0.76	-0.25, 2.98	.093				
betweenness	0.01	0.02	-0.03, 0.05	.717				
age	**-0.35**	**0.15**	**-0.67, -0.02**	**.037**				
rank category	-0.16	0.17	-0.53, 0.22	.383				
full clustering coefficient:					38.99	6.21	0.028	25.91%
Intercept	1.74	2.20	-2.95, 6.44	.442				
clustering coef.	-0.34	3.16	-7.08, 6.41	.917				
age	**-0.35**	**0.15**	**-0.68, -0.03**	**.036**				
rank category	-0.19	0.15	-0.51, 0.12	.209				

full reach:					32.78	0	0.626	44.67%
Intercept	0.15	0.78	-1.52, 1.82	.852				
reach	**1.27**	**0.53**	**0.15, 2.39**	**.029**				
age	**-0.31**	**0.13**	**-0.58, -0.03**	**.034**				
rank category	-0.04	0.14	-0.34, 0.26	.784				
null model:					35.25	2.47	0.182	27.11%
Intercept	1.52	0.62	0.21, 2.82	.025				
age	**-0.35**	**0.15**	**-0.67, -0.04**	**.03**				
rank category	-0.19	0.14	-0.49, 0.11	.196				

Table A V-IV 38 Details on the full and null LMs regarding females' R_{change}, using measures of agonistic network position as predictors (i.e. strength, degree, eigenvector centrality, betweenness centrality, clustering coefficient, and reach). The undirected network was based on all agonistic interactions. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	ΔAIC_C	**ω**	Marginal R^2
full strength:					164.61	3.77	0.063	26.12%
Intercept	-17.62	34.37	-90.88, 55.63	.616				
strength	-4.71	6.04	-17.59, 8.17	.448				
age	-6.64	4.36	-2.65, 15.93	.148				
rank category	4.16	5.61	-7.8, 16.11	.470				
full degree:					165.31	4.48	0.045	23.72%
Intercept	-31.62	41.01	-120.03, 54.8	.439				
degree	-0.32	1.43	-3.37, 2.74	.829				
age	7.5	4.29	-1.65, 16.65	.101				
rank category	6.82	4.46	-2.68, 16.32	.147				
full eigenvector centrality:					165.36	4.52	0.044	23.52%
Intercept	-39.40	32.84	-1009.40, 30.60	.249				
eigenvector cent.	-1.69	34.18	-74.55, 71.17	.961				
age	7.59	4.49	-1.99, 17.16	.112				
rank category	7.02	5.62	-4.97, 19.01	.231				
full betweenness centrality:					163.69	2.85	0.100	29.2%
Intercept	-27.62	20.27	-70.83, 15.58	.193				
betweenness	-0.61	0.52	-1.71, 0.49	-258				
age	7.33	4.07	-1.34, 15.99	.092				
rank category	4.21	4.68	-5.76, 14.18	.382				
full clustering coefficient:					165.31	4.47	0.045	23.7%
Intercept	-28.64	61.19	-159.06, 101.79	.647				
clustering coef.	-18.2	87.88	-205,51, 169.12	.839				
age	7.55	4.27	-1.54, 16.64	.097				
rank category	7.17	4.1	-1.56, 15.9	.101				
full reach: *					160.84	0	0.418	38.05%
Intercept	-7.64	22.76	-56.14, 40.86	.742	(142.01)	(3.21)		(20.05%)
reach	-30.74	15.3	-63.35, 1.87	.063				
age	6.53	3.81	-1.58, 14.64	.107				
rank category	3.49	4.08	-5.20, 12.19	.405				
null model:					161.61	0.77	0.285	24.69%
Intercept	-40.77	17.11	-77.04, -4.51	.03	(138.80)	(0)		(18.28%)
age	7.66	4.10	-1.04, 16.36	.081				
rank category	7.21	3.97	-1.19, 15.62	.088				

*** rip influential data point** (AIC_C and effect sizes of models without influential data point in brackets)

Table A V-IV 39 Details on the full and null LMs regarding females' R_{change} after the influential data point marked in Table A V-IV 38 was removed, using measures of agonistic network position as predictors (i.e. reach). The undirected network was based on all agonistic interactions. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	Marginal R^2
full reach:					142.01	3.21	20.05%
Intercept	-33.57	18.03	-72.24, 5.1	.984			
reach	12.06	16	-22.25, 46.37	.463			
age	2.49	2.99	-3.91, 8.89	.428			
rank category	6.01	3.06	-0.55, 12.56	.07			
null model:					138.80	0	18.28%
Intercept	-23.48	11.90	-48.85, 1.89	.067			
age	2.86	2.90	-3.33, 9.04	.341			
rank category	4.93	2.67	-0.76, 10.61	.084			

Table A V-IV 40 Details on the full and null LMs regarding females' R_{temp}, using measures of agonistic network position as predictors (i.e. strength, degree, eigenvector centrality, betweenness centrality, clustering coefficient, and reach). The undirected network was based on all agonistic interactions. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC$_C$	Δ AIC$_C$	ω	Marginal R^2
full strength:					63.96	0	0.336	6.12%
Intercept	-1.36	2.05	-5.83, 3.12	.521				
strength	0.48	0.50	-0.61, 1.57	.358				
age	0.03	0.49	-1.04, 1.10	.953				
full degree: *****					68.54	4.58	0.034	6.06%
Intercept	-5.32	5.85	-18.2, 7.55	.382	(57.20)	(2.93)		(39.21%)
degree	0.17	0.19	-0.24, 0.58	.372				
age	0.14	0.53	-1.03, 1.32	.794				
rank category	0.47	0.7	-1.06, 2	.514				
full eigenvector centrality:					64.1	0.14	0.314	5.38%
Intercept	-1.16	1.97	-5.45, 3.14	.569				
eigenvector cent.	2.51	2.81	-3.61, 8.63	.390				
age	0.05	0.5	-1.03, 1.13	.920				
full betweenness centrality: *****					67.04 (54.27)	3.08 (0)	0.072	13.35% (49.34%)
Intercept	-2.4	2.57	-8.06, 3.27	.372				
betweenness	0.09	0.06	-0.05, 0.23	.174				
age	-0.02	0.49	-1.09, 1.06	.974				
rank category	0.65	0.66	-0.81, 2.11	.350				
full clustering coefficient:					69.60	5.64	0.020	0.64%
Intercept	-1.93	7.31	-18,03, 14.26	.796				
clustering coef.	2.53	10.72	-21.06, 26.13	.818				
age	0.02	0.54	-1.16, 1.20	.970				
rank category	0.09	0.61	-1.24, 1.43	.879				
full reach:					69.2	5.24	0.025	2.75%
Intercept	-1.63	3.2	-8.67, 5.40	.619				
reach	1.25	2.08	-3.33, 5.82	.561				
age	0.01	0.52	-1.15, 1.16	.992				
rank category	0.30	0.67	-1.18, 1.79	.660				
null model:					65.01	1.05	0.199	0.27%
Intercept	-0.20	2.23	-5.15, 4.56	.897	(58.36)	(4.09)		(13.22%)
age	0.001	0.51	-1.11, 1.11	.998				
rank category	0.11	0.58	-1.15, 1.37	.849				

*** nor influential data point** (AIC$_C$ and effect sizes of models without influential data point in brackets)

Table A V-IV 41 Details on the full and null LMs regarding females' R_{temp} after the influential data points marked in Table A V-IV 40 were removed, using measures of agonistic network position as predictors (i.e. degree and betweenness centrality). The undirected network was based on all agonistic interactions. Models included age and rank category.

Fixed effect	estimate	SE	95%-CI	p-value	AIC_C	Δ AIC_C	Marginal R^2
full degree:					57.20	2.93	39.21%
Intercept	-13.81	5.11	-25.2, -2.43	.022			
degree	**0.35**	**0.15**	**0.02, 0.69**	**.04**			
age	0.31	0.40	-0.58, 1.20	.457			
rank category	**1.94**	**0.7**	**0.39, 3.49**	**.019**			
full betweenness centrality:					54.27	0	49.34%
Intercept	-6.7	2.19	-11.57, -1.83	.012			
betweenness	**0.14**	**0.05**	**0.04, 0.25**	**.013**			
age	-0.01	0.34	-0.77, 0.76	.983			
rank category	**2.00**	**0.61**	**0.65, 3.36**	**.008**			
null model:					58.36	4.09	13.22%
Intercept	-2.63	2.28	-7.66, 2.39	.274			
age	0.01	0.45	-0.98, 1.01	.974			
rank category	0.9	0.64	-0.51, 2.31	.188			

AGONISM NETWORK – PERMUTATION TESTS

Table A V-IV 42 Details on the permutation procedure regarding the link between males' R_{coat} and their degree in an agonistic network. The undirected network was based on all agonistic interactions, node permutations were repeated 1000 times. Models included age, while rank category was excluded due to VIFs > 2 between rank and degree.

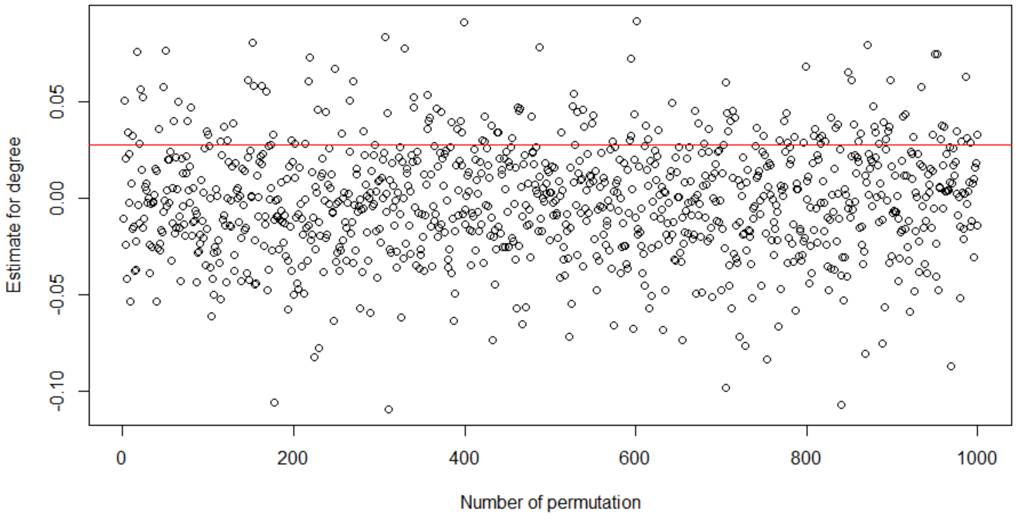
Network metric: degree
Model: R_{coat} ~ degree + age
Proportion observed est. < randomised est.: 0.145


Table A V-IV 43 Details on the permutation procedure regarding the link between males' R_{change} and their degree in an agonistic network. The undirected network was based on all agonistic interactions, node permutations were repeated 1000 times. Models included age, while rank category was excluded due to VIFs > 2 between rank and degree.

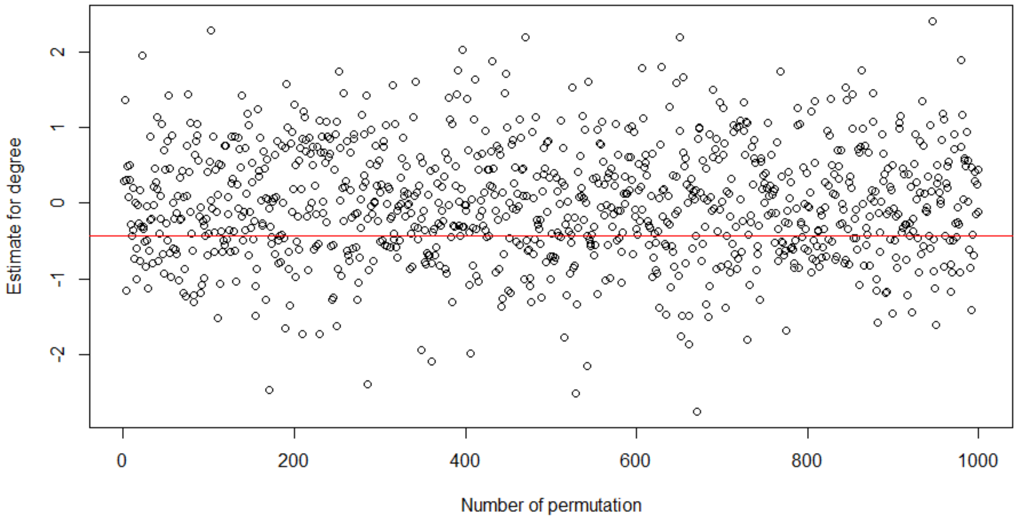
Network metric: degree
Model: R_{change} ~ degree + age
Proportion observed est. < randomised est.: 0.705


Table A V-IV 44 Details on the permutation procedure regarding the link between males' R_{change} and their betweenness centrality in an agonistic network. The undirected network was based on all agonistic interactions, node permutations were repeated 1000 times. Models included age and rank.

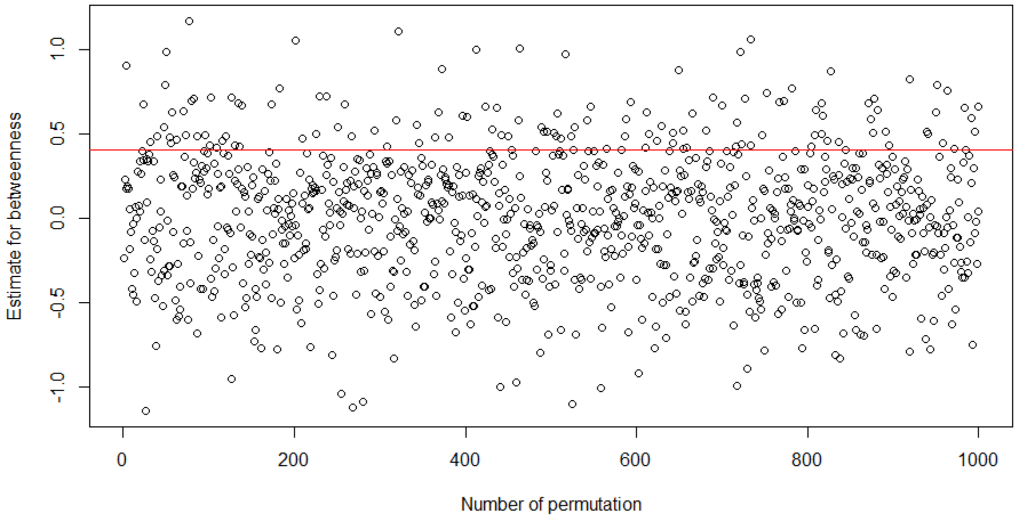
Network metric: betweenness centrality
Model: R_{change} ~ betweenness centrality + age + rank
Proportion observed est. < randomised est.: 0.134


Table A V-IV 45 Details on the permutation procedure regarding the link between males' R_{temp} and their degree in an agonistic network. The undirected network was based on all agonistic interactions, node permutations were repeated 1000 times. Models included age, while rank category was excluded due to VIFs > 2 between rank and degree.

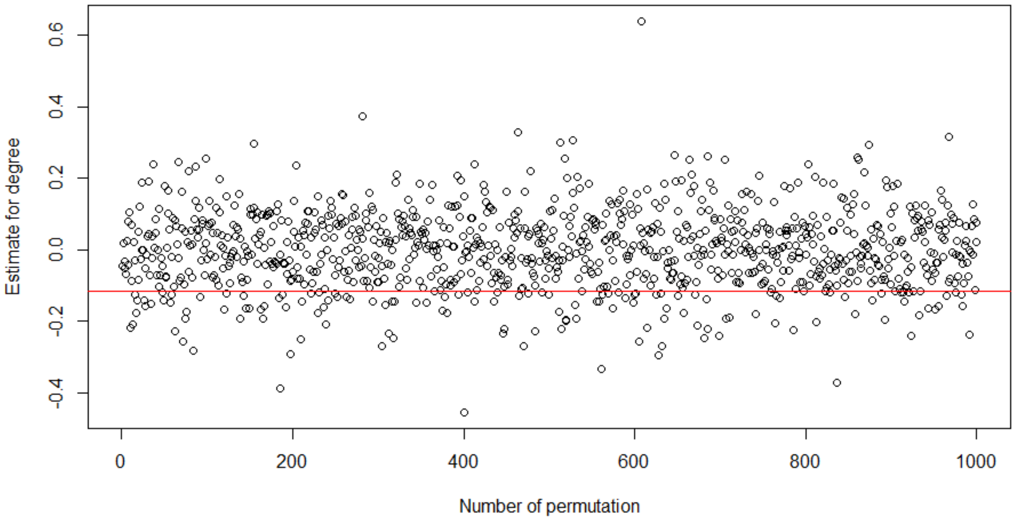
Network metric: degree
Model: R_{temp} ~ degree + age
Proportion observed est. < randomised est.: 0.866


Table A V-IV 46 Details on the permutation procedure regarding the link between males' R_{temp} and their clustering coefficient in an agonistic network. The undirected network was based on all agonistic interactions, node permutations were repeated 1000 times. Models included age and rank.

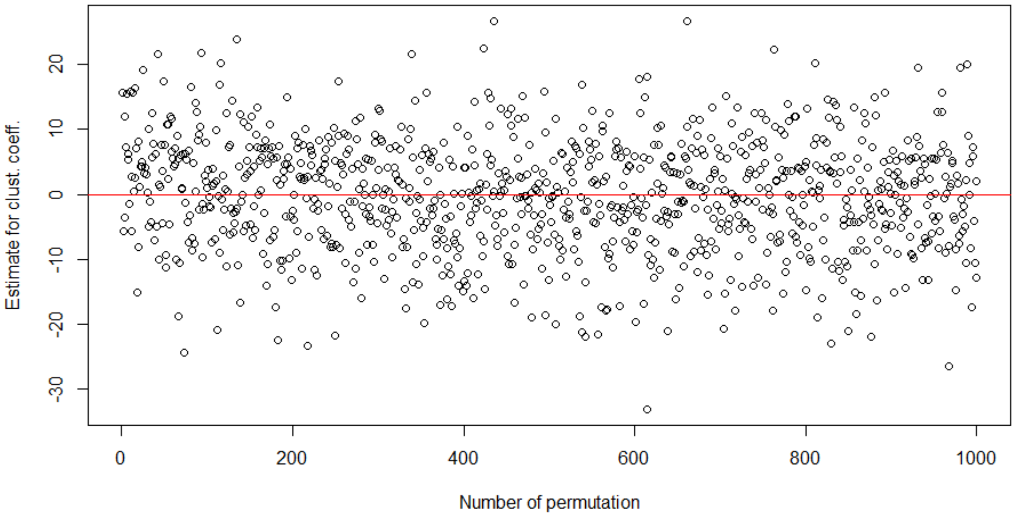
Network metric: individual clustering coefficient
Model: R_{temp} ~ individual clustering coefficient + age + rank
Proportion observed est. < randomised est.: 0.502


Table A V-IV 47 Details on the permutation procedure regarding the link between males' R_{temp} and their reach in an agonistic network. The undirected network was based on all agonistic interactions, node permutations were repeated 1000 times. Models included age and rank.

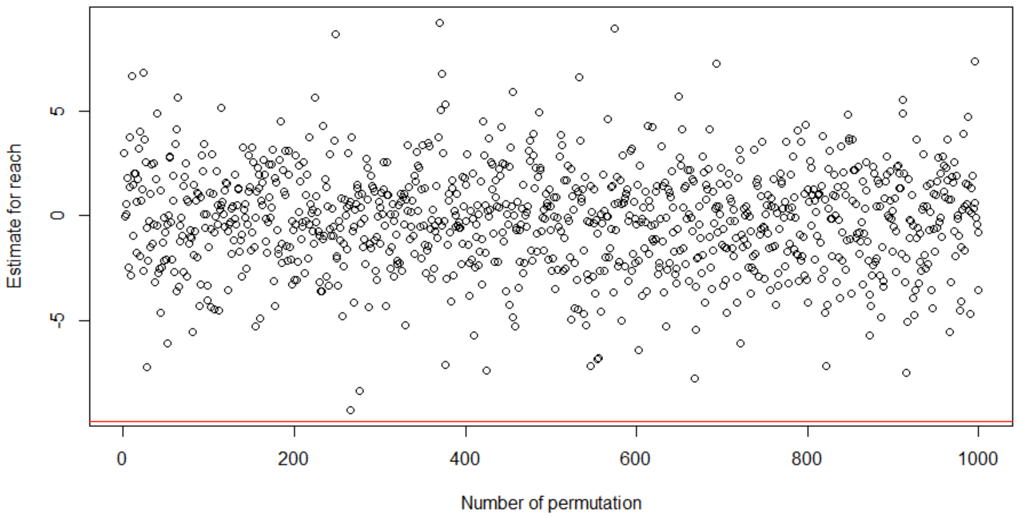
Network metric: reach
Model: R_{temp} ~ reach + age + rank
Proportion observed est. < randomised est.: 1


Table A V-IV 48 Details on the permutation procedure regarding the link between females' R_{coat} and their reach in an agonistic network. The undirected network was based on all agonistic interactions, node permutations were repeated 1000 times. Models included age and rank.

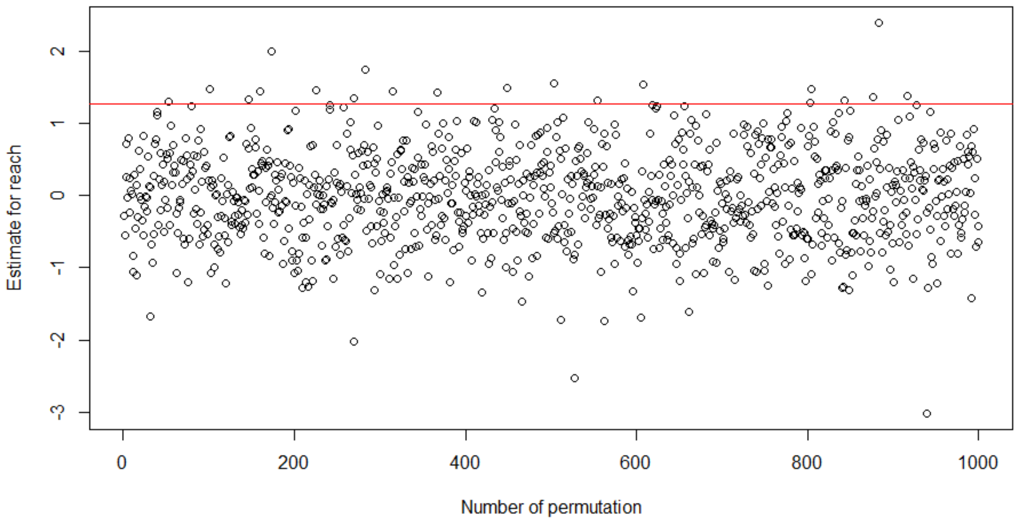
Network metric: reach
Model: R_{coat} ~ reach + age + rank
Proportion observed est. < randomised est.: 0.02


Table A V-IV 49 Details on the permutation procedure regarding the link between females' R_{change} and their reach in an agonistic network. The undirected network was based on all agonistic interactions, node permutations were repeated 1000 times. Models included age and rank.

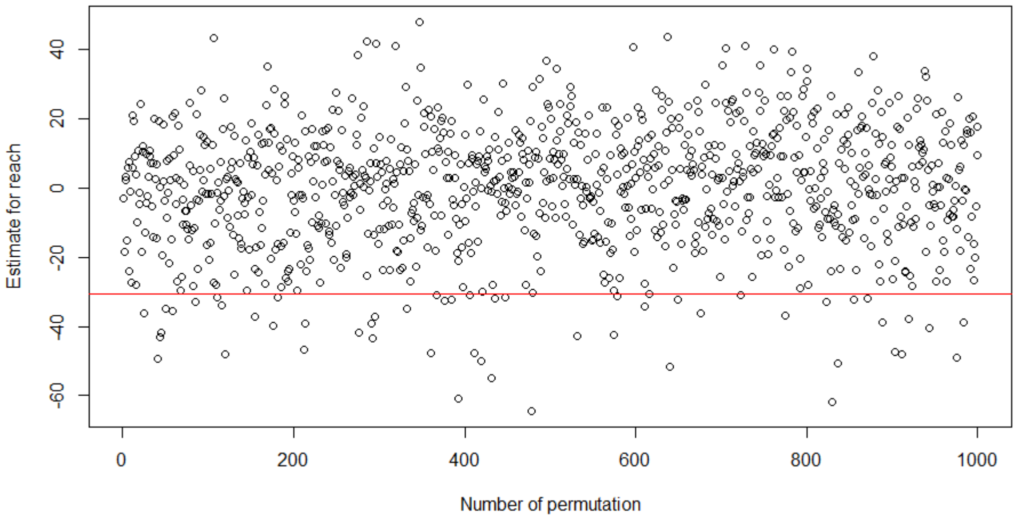
Network metric: reach
Model: R_{change} ~ reach + age + rank
Proportion observed est. < randomised est.: 0.946


Table A V-IV 50 Details on the permutation procedure regarding the link between females' R_{temp} and their strength in an agonistic network. The undirected network was based on all agonistic interactions, node permutations were repeated 1000 times. Models included age, while rank category was excluded due to VIFs > 2 between rank and strength.

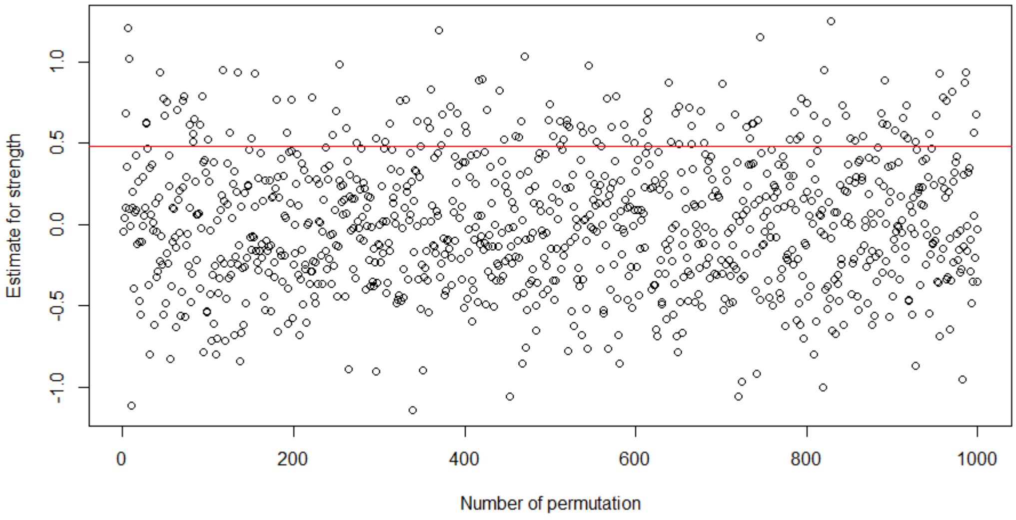
Network metric: strength
Model: R_{temp} ~ strength + age
Proportion observed est. < randomised est.: 0.14


Table A V-IV 51 Details on the permutation procedure regarding the link between females' R_{temp} and their degree in an agonistic network. The undirected network was based on all agonistic interactions, node permutations were repeated 1000 times. Models included age and rank.

Network metric: degree

Model: R_{temp} ~ degree + age + rank

Proportion observed est. < randomised est.: 0.072

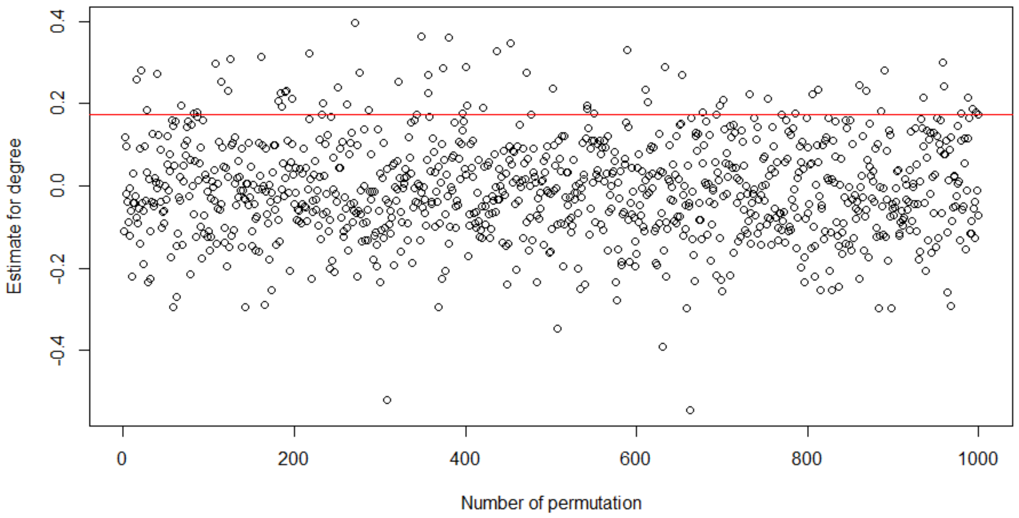


Table A V-IV 52 Details on the permutation procedure regarding the link between females' R_{temp} and their eigenvector centrality in an agonistic network. The undirected network was based on all agonistic interactions, node permutations were repeated 1000 times. Models included age, while rank category was excluded due to VIFs > 2 between rank and eigenvector centrality.

Network metric: eigenvector centrality

Model: R_{temp} ~ eigenvector centrality + age

Proportion observed est. < randomised est.: 0.058

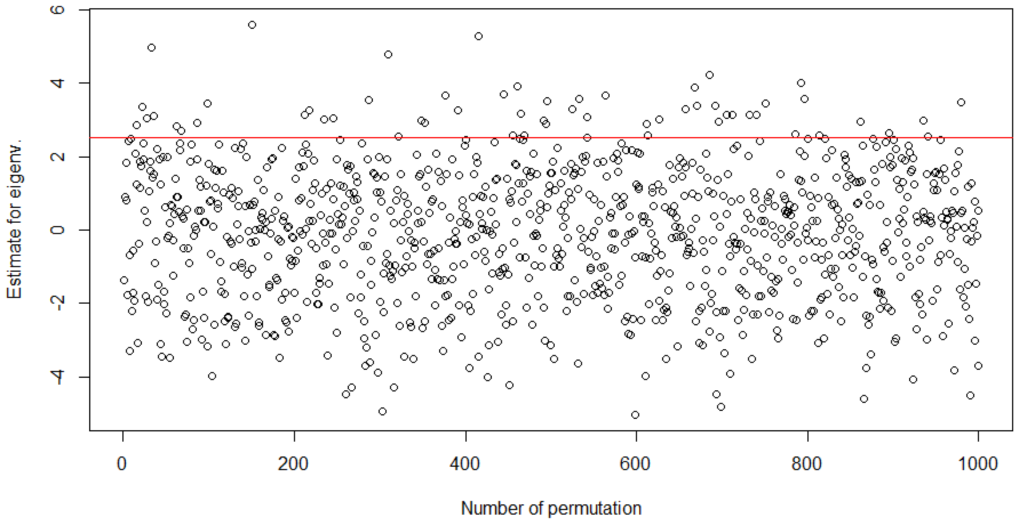
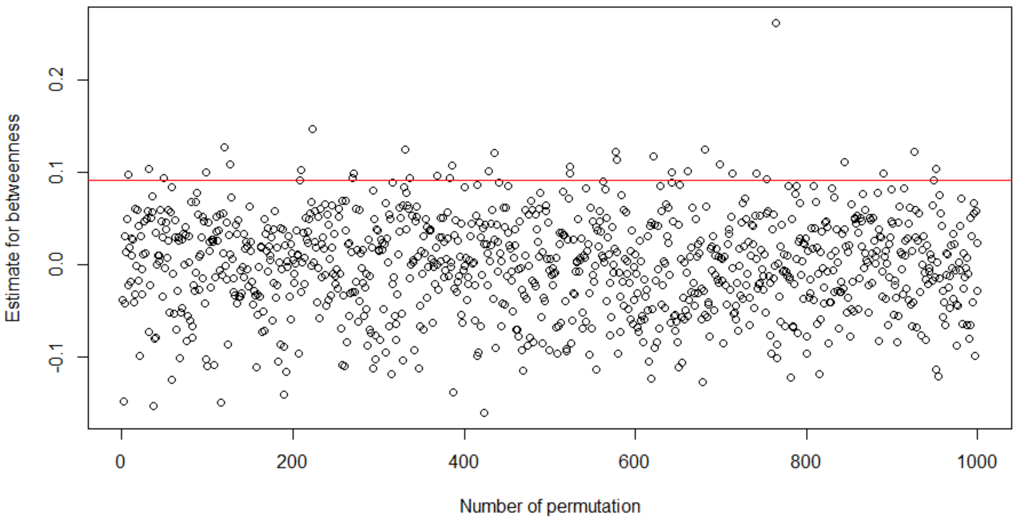


Table A V-IV 53 Details on the permutation procedure regarding the link between females' R_{temp} and their betweenness centrality in an agonistic network. The undirected network was based on all agonistic interactions, node permutations were repeated 1000 times. Models included age and rank.

Network metric: betweenness centrality
Model: R_{temp} ~ betweenness centrality + age + rank
Proportion observed est. < randomised est.: 0.034


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