

**Grunt usage and social monitoring:
Investigation of the signaller and the receiver
perspectives in a tolerant species of baboons**

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SUMMARY

Understanding society, communication and cognition in non-human primates sheds light on the evolution of our own species. While the acoustic structure in primates is mainly innate, their vocal usage and comprehension/response are more flexible and fluctuate based on social experiences. Because relationships can vary between individuals within the same group and change over time, the contexts of call usage (signaller perspective) and the patterns of response to vocalisations (receiver perspective) is supposed to differ even among closely related species.

My thesis project is in line with the current framework investigating to which degree social system shapes communication and social cognition in primates. More specifically, I studied the usage of an affiliative vocalisation – the ‘grunt’ – and the allocation of social attention of a wild population of Guinea baboons (*Papio papio*) living in the Niokolo Koba National Park, Senegal. By combining behavioural observations and experimental designs, I investigated the perspectives of the signaller and the receiver focusing on the grunt, the most common affiliative vocalisation in baboons. Savannah baboons (*P. ursinus*, *P. cynocephalus*, *P. kinda*, *P. anubis*) live in polygynandrous groups characterized by high male-male competition and stable female-bonded societies. In contrast, the social organization of Guinea and hamadryas baboons (*P. hamadryas*) is defined by a nested multi-level society, female-biased dispersal and a polygyny-monandrous mating system. In Guinea baboons, the ‘unit’ — i.e., a ‘primary’ male, 1-6 females, their youngster, and frequently ‘secondary’ males — represents at the core of the society, and the agglomeration of several units is called a ‘party’. Males are mainly philopatric within a party and share high spatial tolerance, facilitating the formation of strong and enduring social bonds.

To investigate if the social system of Guinea baboons influences their grunt usage, I collected behavioural observations of sexually mature males and females. First, I examined if the nature of post-approach interactions was modulated by the grunt production of the approaching animal (i.e., the subject). Following approaches with grunts in both sexes, the dyad was more likely to interact in an affiliative way. Moreover, grunts increased the probability of manipulation of the partner’s infant and reduced the risk of displacement. Subsequently, I tested how infants in close-proximity of the receiver and the quality of relationships between the partners potentially influence the subject’s decision to grunt or to remain silent. Both sexes were more likely to grunt to female than to male partners. Between females, the probability of vocal production was lower when the relationship strength was high, but only when an infant was present with her partner. The unit membership also impacted the grunt utterance as females were more likely to vocalise while approaching a female from a different unit. Dominance status and dyadic rank distance did not affect the probability to grunt between females, even if a linear dominance hierarchy was

detected. In correspondence with the high tolerance between males of this species, relationship strength had no impact on the likelihood to grunt during male-male approaches. Finally, males were more likely to grunt when an infant was in close-proximity of the female partner. Overall, these results indicate that Guinea baboons use grunts strategically to advertise their benign intent during specific unpredictable situations (e.g., while approaching non-preferential partners). Although genetic constraints limit the structure and extent of vocal repertoire within taxa, baboons can adapt their vocal usage flexibly depending on their social environment.

In a second study, I explored the receiver perspective in adult male Guinea baboons by testing the attention to third-party social interactions. I carried out playback experiments to assess if males keep track of the current pattern of male-female associations within their own party (but outside their own unit). First, I established that grunts occur more frequently between females and primary males of the same unit than from different units. Then, I created consistent and inconsistent acoustic sequences simulating grunt exchanges between a female and a primary male from the same or from different units respectively. I tested those grunt sequences on primary and non-primary males, as male status (association with a female) could influence the value of the social information. Surprisingly, male Guinea baboons looked longer toward the speaker when exposed to the consistent compared to the inconsistent condition, a result opposite to comparable playback experiments on chacma baboon males. Moreover, primary males reacted more than non-primary males regardless of the experimental condition. Thus, this result reveals how differences of the mating system and the degree of male competition affect the value allocated to social information even between closely related species.

By comparing my results with the literature on geladas and other baboon species, the variations observed in call usage and the motivation to keep track of third-party interactions in Guinea baboons are likely to be related to different aspects of their social systems. Although Guinea baboons use grunts strategically to signal benign intent, like in many other primate species, the lack of a significant effect of male-male and male-female bond strength, as well as female dominance hierarchy on grunt utterance may be related to the low competition level observed both within and between sexes in this species. Considering the low interest toward recordings of simulated incongruent male-female associations, my playback experiments support that the allocation of social attention — and potentially the extent of social knowledge — is highly dependent on the mating system and the level of competition/tolerance among conspecifics. Future research should consider a set of measures to reveal how the competition, cohesion and/or cooperation potentially impact the evolution of communication and cognition. Furthermore, extensive comparative investigations across species and populations fluctuating in

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some dimensions of their social systems are necessary, as the social environment seems to account for more variation among species than genetic relatedness.

RÉSUMÉ

La compréhension des sociétés, de la communication et de la cognition chez les primates non humains permet de mieux comprendre l'évolution de notre propre espèce. Bien que la structure acoustique chez les primates soit principalement innée, leur utilisation vocale et leur compréhension / réponse sont plus flexibles et fluctuent en fonction des expériences sociales. Comme les relations peuvent varier entre les individus d'un même groupe et changer avec le temps, les contextes d'utilisation des vocalisations (perspective du signaleur) et les schémas de réponse aux vocalisations (perspective du récepteur) sont supposés différer même entre espèces très proches.

Mon projet de thèse s'inscrit dans le cadre actuel déterminant dans quelle mesure le système social façonne la communication et la cognition sociale chez les primates. Plus spécifiquement, j'ai étudié l'utilisation d'une vocalisation affiliative — le grognement — et la surveillance sociale d'une population sauvage de babouins de Guinée (*Papio papio*) vivant dans le parc national du Niokolo Koba, au Sénégal. En combinant des observations comportementales et des designs expérimentaux, je me suis attachée à investir le point de vue du signaleur et du receveur en utilisant le grognement, la vocalisation affiliative la plus commune chez les babouins. Les babouins de savane (*P. ursinus*, *P. cynocephalus*, *P. kinda*, *P. anubis*) vivent dans des groupes polygynandres caractérisés par une forte compétition entre mâles et des relations sociales stables entre femelles. À l'inverse, l'organisation sociale des babouins de Guinée et hamadryas (*P. hamadryas*) est caractérisée par une société à plusieurs niveaux, une dispersion majoritaire des femelles et un système reproductif polygyny-monandre. Chez le babouin de Guinée, « l'unité » — i.e., un mâle « primaire », 1-6 femelle, leur progéniture, et fréquemment des mâles « secondaires » — représente le cœur de la société, et l'agglomération de plusieurs unités s'appelle le « parti ». Les mâles sont majoritairement philopatriques au sein d'un parti et partagent une grande tolérance spatiale, facilitant la formation de liens sociaux forts et durables.

Afin d'évaluer si le système social du babouin de Guinée influence leur utilisation du grognement, j'ai collecté des observations comportementales de mâles et de femelles sexuellement matures. Tout d'abord, j'ai examiné si la nature des interactions suite à une approche était modulée par la production de grognements par l'animal approchant (i.e., le sujet). À la suite d'une approche avec grognement chez les deux sexes, la dyade était plus susceptible d'interagir de manière affiliative. De plus, les grognements augmentaient la probabilité de manipulation du nourrisson du partenaire et réduisaient le risque de supplantation. Par la suite, j'ai testé comment un nourrisson à proximité du receveur et la qualité des liens sociaux entre partenaires pouvaient potentiellement influencer la décision du sujet à grogner ou rester silencieux. Les deux sexes étaient plus susceptibles de grogner envers un partenaire féminin que

masculin. Entre femelles, la probabilité d'émission vocale était plus faible lorsqu'elles partageaient de forts liens sociaux, et ceci uniquement en présence d'un nourrisson avec sa partenaire. L'appartenance à une unité a également eu un impact sur le grognement, car les femmes étaient plus susceptibles de vocaliser lorsqu'elles approchent une femme d'une autre unité. Le statut de dominance et l'écart entre rang hiérarchique dyadique n'altéraient pas la probabilité de grognement entre femelles, même si une hiérarchie de dominance linéaire a été démontrée. En accord avec la tolérance élevée chez les mâles de cette espèce, la force des liens sociaux n'a eu aucun impact sur la probabilité de grogner lors d'approches entre mâles. Enfin, les mâles étaient plus prompts à grogner lorsqu'un nourrisson était à proximité du partenaire féminin. Dans l'ensemble, ces résultats indiquent que les babouins de Guinée utilisent les grognements de manière stratégique pour faire connaître leurs intentions bénignes lors de situations imprévisibles spécifiques (par exemple, en s'approchant d'un partenaire non préférentiel). Bien que les contraintes génétiques limitent la structure et l'étendue du répertoire vocal au sein d'un même taxon, les babouins peuvent adapter leur utilisation vocale de manière flexible en fonction de leur environnement social.

Dans une seconde étude, j'ai exploré le point de vue du receveur en testant l'attention portée aux interactions sociales de tiers chez les mâles adultes babouins de Guinée. J'ai pratiqué des expériences de repasse pour déterminer si les mâles suivaient les associations actuelles entre mâles et femelles au sein de leur parti (mais en dehors de leur propre unité). Tout d'abord, j'ai démontré que les grognements sont exprimés plus fréquemment entre femelles et mâles primaires d'une même unité que d'unités différentes. Par la suite, j'ai réalisé des séquences acoustiques congruentes et incongrues simulant un échange de grognements entre une femelle et un mâle primaire appartenant respectivement à la même unité ou non. J'ai testé ces séquences de grognements sur des mâles primaires et des mâles non primaires, comme le statut des mâles (association avec une femelle) pourrait influencer la valeur des informations sociales. Étonnamment, les babouins mâles regardaient plus longtemps vers le hautparleur lorsqu'ils étaient exposés à la condition congruente par rapport à la condition incongrue, un résultat opposé à une précédente expérience de repasse chez le mâle babouin chacma. De plus, les mâles primaires réagissaient plus fortement que les mâles non primaires, quel que soit la condition expérimentale. Ainsi, ces résultats révèlent comment les différences du système reproductif et du degré de compétition entre mâles affectent la valeur allouée aux informations sociales même entre espèces génétiquement proches.

En comparant mes résultats avec la littérature chez les geladas et d'autres espèces de babouins, les variations observées lors de l'utilisation de vocalisations et la motivation à suivre les interactions des autres chez les babouins de Guinée sont susceptibles d'être liées à des

caractéristiques propres à leur système social. Bien que les babouins de Guinée utilisent des grognements de manière stratégique pour signaler leur intention bienveillante, comme c'est le cas chez plusieurs autres espèces de primates, l'absence de significativité de la force des liens sociaux entre mâles et mâles-femelles, ainsi que de la hiérarchie de dominance féminine sur la production de grognements pourrait être liée au faible niveau de compétition observé à la fois entre ou au sein d'un même sexe chez cette espèce. Compte tenu du faible intérêt que suscitent les enregistrements simulant des associations incongrues entre femelles et mâles, mes expériences de repasse supportent que l'attribution de l'attention sociale — et potentiellement l'étendue des connaissances sociales — dépend fortement du système reproductif et du degré de compétition/tolérance entre congénères. De futures recherches devraient considérer un ensemble de mesures révélant comment la compétition, la cohésion et la coopération impact potentiellement l'évolution de la communication et de la cognition. De plus, le développement de recherches comparatives entre espèces ou populations confrontées à des fluctuations des différentes dimensions du système social est primordial, sachant que l'environnement social semble expliquer davantage de variation entre espèces que les relations génétiques.

CHAPTER 1 – General introduction

Understanding the relationships existing among sociality, communication and cognition (see Shettleworth, 2010 for definition) in non-human primates (hereafter ‘primates’) offers important insights into human evolution. Indeed, as archaeological evidence is scarce (e.g., Jolly, 2001), comparative investigations of modern human hunter-gatherer societies (Dyble et al., 2017) as well as our closest relatives (e.g., Swedell & Plummer, 2012) allow scientists to understand the phylogenetic origins and the potential adaptive functions of those traits in response to specific ecological conditions (Maestriperi, 2005).

Primates are also interesting research models as they live in diverse social (and ecological) environments differing in their social systems — from the solitary orang-utan to the highly gregarious gelada (Mitani, Call, Kappeler, Palombit, & Silk, 2013). Typically, the social system (or society) is divided in three different components (Kappeler & van Schaik, 2002), namely the social organisation (i.e., size, sex ratio and cohesion of a group), the mating system (i.e., mating interactions and their reproductive consequences) and the social structure (i.e., nature and distribution of social interactions among group members). Furthermore, extensive work in natural and experimental settings provided insight into the extended cognitive skills primates exhibit while confronted to social or physical problems (e.g., Cheney & Seyfarth, 2007). Using an evolutionary approach, this thesis aims to understand how the differing demands of social systems impact communication (e.g., Dobson, 2012; Owren, Dieter, Seyfarth, & Cheney, 1993) and social cognition (e.g., Hare, Melis, Woods, Hastings, & Wrangham, 2007; Joly, Micheletta, Langermans, Sterck, & Waller, 2017), by studying the vocal usage and the attention processes of a tolerant species of baboon, the Guinea baboon (*Papio papio*).

In the following paragraphs, I will provide a brief overview on the social theory regarding the evolution of brain enlargement (**section 1.1.**), describe vocal communication with a main focus on primate calls (**section 1.2.**), review two facets of social cognition — namely individual recognition and third-party knowledge — (**section 1.3.**), present the current state of knowledge on the social system of our study species (**section 1.4.**) and outline the main aspects of social cognition specifically investigated within this PhD thesis (**section 1.5.**).

1.1. Sociality, cognition and brain size enlargement

Despite the prolonged periods of neurodevelopment and the metabolic cost of brain maintenance (Isler & Van Schaik, 2006), natural selection has favoured larger brain volume — relative to body mass — in the order Primates. Although the majority of work on this topic has focused on primates, it became clear that large brain size has also been demonstrated in some non-primate mammals and birds (Benson-Amram, Dantzer, Stricker, Swanson, & Holekamp,

2016; Marino et al., 2006; Sol, Duncan, Blackburn, Cassey, & Lefebvre, 2005). Several theories have been proposed to reveal which selective pressures could have promoted the expansion of brain volume, assumed to co-vary with higher socio-cognitive skills.

Historically, some of the most widely supported hypotheses on the evolution of larger brain volume maintain that sociality acts as a major driver of brain expansion. The first article indicating that sociality influenced the enhanced intellect of simians was published by Jolly (1966). Later on, the ‘Machiavellian Intelligence’ hypothesis (Byrne & Whiten, 1988) or ‘Social Intelligence’ (Barton & Dunbar, 1997) stipulates that intelligence evolved in response to the competitive social environments in which animals should use tactical deception to steal valuable resources from others (see also the ‘Social Intellect’ theory in Humphrey, 1976). As the usage of others’ behaviours is not necessarily deceptive and manipulative, other variants, namely the ‘Social Brain’ (Dunbar, 1998) or ‘Social Complexity’ hypothesis (Connor, Smolker, & Richards, 1992), proposed that brain enlargement evolved to cope with the challenges of living in complex social groups with fluctuating social roles between conspecifics and over time. Indeed, animals face multiple challenges when dealing with diverse social problems such as making predictions about conspecifics’ behaviours, utilising these predictions for personal gain or to facilitate coordination, and recognising relationships among conspecifics (Jensen et al., 2011).

Multiple quantitative social proxies have been correlated with the expansion of brain volume (reviewed in Healy & Rowe, 2007) such as group size (Dunbar, 1992), female cohort size (Lindenfors, Nunn, & Barton, 2007), rate of alliances (Dunbar & Shultz, 2007a) and agonistic interactions (Cowl & Shultz, 2017). Furthermore, social organization characterised by high degree of fission-fusion dynamics is supposed to pressure to communicative and cognitive processes, such as the ability to mentally represent and monitor oneself and others (Amici, Aureli, & Call, 2008; reviewed in Aureli, Schaffner, Boesch, Bearder, Call, Chapman, Connor, Di Fiore, et al., 2008). Finally, some evidence highlights the potential impacts of the level of despotism/tolerance on social cognition (e.g., Hare et al., 2007; Joly et al., 2017). For instance, bonobos (*Pan paniscus*) perform better in cooperative tasks (e.g., two individuals pulling together a platform with clumped food items) than chimpanzee (*Pan troglodytes*) displaying a lower degree of social tolerance (Hare et al., 2007). Overall, the natural selection has favoured individuals equipped with sophisticated cognitive abilities (e.g., behavioural flexibility and social knowledge) for making proper decisions about when and whom to compete and/or cooperate with. As a consequence, it has been suggested that those decisions provide long-term fitness benefits, such as ascending in the dominance hierarchy (Gilby et al., 2013; Schülke, Bhagavatula, Vigilant, & Ostner, 2010), enhancing longevity and reproductive success (McFarland & Majolo, 2013; Silk et al., 2010; Silk, Alberts, & Altmann, 2003).

Uncertainty remains over which social factors are of greatest importance in the brain evolution. In response to this last methodological issue, more reliable measures for thoroughly quantifying the complexity of social systems are sought after. For instance, one social variable more likely to shape social cognition is the ability to track a ‘number of differentiated relationships’ with and between conspecifics (Bergman & Beehner, 2015). Indeed, more advanced cognitive skills are required as the number of differentiated relationships to process increases, as primates must recognize and maintain their relationships and follow fluctuating social information transmitted between other dyads over time. Several measures of social relationships, such as the strength of affiliative bonds (e.g., Dyadic Composite Sociality Index: Silk, Cheney, & Seyfarth, 2013) or the relative rank (e.g., ELO-rating: Albers & de Vries, 2001), as well as cluster (Fischer, Farnworth, Sennhenn-Reulen, & Hammerschmidt, 2017) or social network analysis (Boyer & Ramos-Fernández, 2018), can be used to quantify the degree of differentiation between relationships across group members.

1.2. Vocal communication

Generally, communication evolved to transmit a signal from a sender to one or several receivers to elicit a behavioural and/or a physiological response (Dawkins & Krebs, 1978; Fischer, 2011). When the signaller and/or the receiver benefit from the emission of a signal, and interact repeatedly, communication is more likely to become an evolutionary stable strategy (ESS: Maynard Smith, 1978). However, following the Machiavellian hypothesis (Byrne & Whiten, 1988), animals do not exclusively cooperate but also compete and, therefore, there are often cases where the sender manipulates the recipient to its own advantage (see **section 1.2.2.2.**). To investigate the signaller perspective, studies focused commonly on two main aspects of vocal communication (Seyfarth & Cheney, 2010), namely the structure (**section 1.2.1.**) and the usage of calls (**section 1.2.2.**).

1.2.1. Fixed and limited vocal repertoire

While modern human language (Fitch, 2010) and vocal signalling in birds (i.e., hummingbirds, songbirds and parrots: Janik & Slater, 2000) and some non-primate mammals (cetacean: Janik, 2014; bat: Knörnschild, Nagy, Metz, Mayer, & Von Helversen, 2010) are mainly acquired through auditory inputs, vocal structure (i.e., spectro-temporal features of a call: Seyfarth & Cheney, 2010) in primates appears to be genetically constrained and principally modulated by body weight and hormones. Since acoustic structures are strongly innate, primates can produce adult-like species-specific vocalisations from birth, even if they are congenitally deaf, raised by another species (i.e., cross-fostering) or a deaf mother, or completely deprived of any interaction

with conspecifics (reviewed in Hammerschmidt & Fischer, 2008). This strong genetic predisposition has also been shown to occur in hybrid specimens, which utter intermediate acoustic structures (e.g., *Hylobates pileatus* and *H. lar*: Geissmann, 1984), and in closely related species sharing comparable acoustic structures within call types and vocal repertoire size (e.g., baboons: Hammerschmidt & Fischer, 2019). Under these circumstances, it seems that primates do not have the ability to modify or create new signals in their vocal structure.

Although the vocal repertoire is strongly constrained, few studies report that primates have some control over their vocal structure based on learned experiences. For example, primates are capable of modulating the spectro-temporal features of their calls, such as the call length, amplitude (known as the ‘Lombard effect’, see Brumm & Zollinger, 2011 for review) and rate of production (Egnor, Wickelgren, & Hauser, 2007; Ey, Rahn, Hammerschmidt, & Fischer, 2009). Those adjustments are crucial to avoid interferences with other sounds of the environment, and the general structure of the habitat (close versus open) which modulates sounds propagation. Moreover, support in favour of this hypothesis has come from studies documenting convergence (or divergence) of acoustic parameters. Indeed, the presence of ‘dialects’ at the population level (Schlenker et al., 2014; Watson et al., 2015; but see Fischer, Wheeler, & Higham, 2015) and vocal ‘accommodation’ (i.e., vocal matching and vocal mimicry) between favourite social peers has been found in primates (Briseno-Jaramillo, Ramos-Fernández, Palacios-Romo, Sosa-López, & Lemasson, 2018; Ruch, Zürcher, & Burkart, 2018). Moreover, some cases of vocal innovation has been suggested on captive populations (Lameira, Hardus, Mielke, Wich, & Shumaker, 2016).

1.2.2. Flexibility of call usage

Compared to their rather limited acoustic structure, primates can show more plasticity in their vocal usage (i.e., appropriate contexts of production: Seyfarth & Cheney, 2010). Primates seem able to decide whether to vocalise or remain silent depending on the composition of their audience (see **section 1.2.2.2.**) and can even be trained to vocalise on command in response to visual cues (e.g., Hage, Gavrilov, & Nieder, 2013). Moreover, primates seem to delay their own call utterance during vocal exchange (vocal turn-taking: Takahashi, Narayanan, & Ghazanfar, 2013), a phenomena regulated by suppression of the motor neurons (Miller & Wang, 2006). Finally, through repetitive experiences, young individuals learn to express the correct alarm call within a narrow range of predatory stimuli (reviewed by Hollén & Radford, 2009).

However, some authors suggested that this ‘higher’ flexibility of call usage, in comparison with vocal structure, is a reflection of the inner state of the signaller (Borjon, Takahashi, Cervantes, & Ghazanfar, 2016; reviewed in Briefer, 2012). The limited flexibility in the context-specific call usage could be related to strong genetic components (reviewed in Seyfarth & Cheney,

2010). Furthermore, the rules governing call production could be simply driven by the caller's motivational or emotional state (Rendall, 2003; reviewed in Seyfarth & Cheney, 2003), without deliberate intent to inform potential listeners.

1.2.2.1. Contexts of call utterance

Animals use vocal signals in various circumstances, from predator encounter to affiliative interactions. A classic textbook example of context-specific calls comes from the early work of Seyfarth and colleagues (1980), which opened doors for extensive research on the 'meaning' of animal vocalisations. These authors discovered that vervet monkeys (*Cercopithecus aethiops*) give acoustically distinct alarm calls referring to terrestrial and aerial predators, a rudimentary categorisation now documented in several primate and non-primate species (Collier, Radford, Townsend, & Manser, 2017; Zuberbühler, Jenny, & Bshary, 1999). More recently, alarm calls have been shown to convey information about the level of urgency (e.g., Fischer & Price, 2017; Manser, Seyfarth, & Cheney, 2002).

Moreover, studies investigating vocal communication emphasize the importance of vocal signals to mediate spacing patterns. Similarly to songbirds (Morton & Stutchbury, 2012), male primates take part into loud chorus to advertise their relative competitive abilities which may decrease the risk of potential escalating fighting contests over home range, food resources and mating opportunities (Brown & Waser, 2018; Fischer, Kitchen, Seyfarth, & Cheney, 2004; Kitchen, 2004). Indeed, those costly signals, also termed 'badge of status' (see definition by Bergman & Sheehan, 2013), provide 'honest' information about the signaller features: its identity, age, sex, social status and physical condition (reviewed by Ey, Hammerschmidt, Seyfarth, & Fischer, 2007). As a loud vocalisation can be heard by several individuals, long-distance calls may also provide information for potential listening mates (Kitchen, Cheney, & Seyfarth, 2004; Ryan, 1980), and consequently affect indirectly the reproductive success of the signaller.

Using copulations calls (before, during and after the copulation), female primates can advertise their own fertility status and the relative competitive abilities of their mating partner by modifying the rate and the spectro-temporal parameters of copulation calls with respect to ovulation (Higham et al., 2012; reviewed by Pradhan, Engelhardt, Van Schaik, & Maestripieri, 2006). Thus, copulation calls can incite direct mate competition, increasing the likelihood to mate with high-quality males who can protect offspring against infanticidal males in the future (Pradhan et al., 2006).

Because social interactions are only not restricted to sexual and competitive intercourses, animals utter calls to facilitate cooperation, enhanced coordination and mediate interactions when a conflict of interest occurs among conspecifics. Acoustic signals are one of the tools used to

inform others of decisions made about collective movements and synchronise group activity (reviewed in Fischer & Zinner, 2011; Gall & Manser, 2017; Radford, 2004). For example, some primates attempt to begin group movements by producing more or less specific vocal signals (Sperber, Werner, Kappeler, & Fichtel, 2017) or by modifying the rate and intensity of call emission (Watts, 2000). Furthermore, food-associated calls typically attract other group members at the newly discovered feeding site and may even convey information about the nature, palatability or quantity of the food sources (Clay, Smith, & Blumstein, 2012).

Lastly, quiet peaceful vocalisations seem to encourage close-proximity between conspecifics by providing information about the signaller's motivation. In case of uncertainty about the outcome of an interaction, several primate species communicate their dispositions to behave amicably with their partner or with their partner's infant ('benign intent signal': Cheney, Seyfarth, & Silk, 1995b), using low-frequency calls such as 'grunts' or 'girneys' (reviewed in Silk, 2001). Those low-cost signals, also called 'cheap talk' (Silk, Kaldor, & Boyd, 2000), are not context-specific calls, as they are uttered in various situations from feeding to infant handling (Rendall, Seyfarth, Cheney, & Owren, 1999). In some species, grunts can also be used as 'reconciliatory' signals when the aggressor approaches their victim in the aftermath of an agonistic interaction (Cheney & Seyfarth, 1997). As a result of repetitive exposures, listeners can use grunt or girney utterance to reliably predict the nature of subsequent interactions with the signaller. Interestingly, the history of social interactions between signaller and receiver, such as the strength of social bonds, can affect the likelihood to utter those calls (e.g., Silk, Seyfarth, & Cheney, 2016; see **Chapter 2**).

1.2.2.2. Audience effect and deception in call usage

Voluntary control over call usage is conspicuous when bystanders are present. Initially discovered in domestic chickens (*Gallus domesticus*: Marler, Dufty, & Pickert, 1986), this phenomenon called the "audience effect" includes all modifications of the subject behaviours caused by the presence and the composition of the surrounding animals (Seagraves, Arthur, & Egnor, 2016; Toarmino, Wong, & Miller, 2017; see Zuberbühler, 2008 for a brief overview). Empirical support for the audience effect was first investigated in primates by examining the context of alarm calls utterance. Individuals detecting a danger alone tends to remain silent, whereas they often vocalise in presence of conspecifics (e.g., Cheney & Seyfarth, 1985b; but see Cheney & Seyfarth, 1990). Interestingly, male Thomas langurs (*Presbytis thomasi*) keep vocalising until all group members replied to their alarm calls (Wich & de Vries, 2006). Furthermore, callers are sensitive to the identity of nearby conspecifics and utter calls essentially in presence of kin (Pollick, Gouzoules, & De Waal, 2005), preferential (Mitani & Nishida, 1993; Slocombe et al.,

2010), or dominant bystanders (Borgeaud, Schnider, Krützen, & Bshary, 2017; Townsend, Deschner, & Zuberbühler, 2008).

Even if natural selection drives the transmission of honest signalling (Dawkins & Krebs, 1978), data on deceptive acts are relatively common when receivers are unable to detect whether or not the signaller was deceptive or honest (i.e., “tactical deception”: Whiten & Byrne, 1988). Previous studies indicate that primates sometimes suppress their calls when encountering a limited or non-sharable valuable resource to avoid aggression (i.e., food: Hauser, Teixidor, Fields, & Flaherty, 1993; Slocombe et al., 2010; i.e., mate: Le Roux, Snyder-Mackler, Roberts, Beehner, & Bergman, 2013; but see Overduin-de Vries, Olesen, de Vries, Spruijt, & Sterck, 2013). Tufted capuchins (*Cebus apella nigrinus*), for instance, give false alarm calls in non-predatory contexts to distract their conspecifics and thus take advantage of the situation (i.e., prior access to the food resource: Wheeler, 2009). Thus, calls can be strategically uttered to maximise benefits to the caller (e.g., exclusive access to resources, minimize the risk of receiving aggression). However, it cannot be excluded that those vocal adjustments are mediated by the arousal level of the signaller, which may be induced by the presence of higher-ranking individuals for example (Bercovitch, Hauser, & Jones, 1995).

Thus far, these findings emphasize that the patterns of calling underlie a combination of innate and learning-based mechanisms. Despite genetic limitations over acoustic variability, vocalisations do differ in the context of usage and social factors might affect the structure and the context of production of certain calls, even among phylogenetically closely related species (see **Chapter 2**). Moreover, the audience effect highlights that animals keep an eye on the presence, the identity and the behaviours of potential recipients to decide whether to vocalise or not. Consequently, investigating vocal communication provides important insight into animal cognition (e.g., social learning, social knowledge).

1.3. Social knowledge and patterns of response

Whenever a signal is uttered in a predictable social context, the recipient perceives it, processes and stores the social information using several cognitive mechanisms (i.e., recognition of the call given and the rules governing this call usage, identification of the signaller and knowledge associated to this particular individual), and finally acts (Shettleworth, 2010). Thus, investigation of vocal communication should not neglect the receiver perspective, by examining the comprehension of others’ calls (Seyfarth & Cheney, 2010).

In combination with maturational processes, the gradual development of an appropriate response to a particular call requires repetitive exposures to vocal and behavioural reactions of others perceiving this signal (e.g., Fichtel & Van Schaik, 2006; Masataka, 1983). Throughout their

whole life, animals can learn an almost infinite quantity of new sound-meaning pairs, even when those sounds are produced by another species (e.g., Cheney & Seyfarth, 1985; Walton & Kershenbaum, 2018) or an object (e.g., clicker).

In addition to the acquisition of appropriate responses to specific calls, animals gather social information about the status of their conspecifics based on personal experiences and observations of others' interactions (i.e., 'social eavesdropping': McGregor & Dabelsteen, 1996). As some social information changes over time (e.g., relative dominance rank, social bond strength), animals have to monitor and update transient information to navigate in their social environment properly (Cheney & Seyfarth, 2007).

1.3.1. Individual recognition

Individual recognition is a crucial prerequisite of social life and has been adjusted by natural selection. This ability requires an accurate and reliable identification of an individual, based on the learning of individually distinct cues and its categorisation with an appropriate social label (Seyfarth & Cheney, 2009). Individual recognition plays a role in competition and cooperation among animals (e.g., playing 'tit-for-tat': Axelrod, 1981) and the evolution of social behaviours (Hamilton, 1963; Wilson, 1979). This widespread phenomenon in the animal kingdom can be based on one perceptual cue, such as facial and body features, olfactory or vocal signature (reviewed in Tibbetts & Dale, 2007; Wiley, 2013). Furthermore, studies have reported multi-modal facets of individual recognition, suggesting the ability to integrate multisensory representations of specific individuals (Gilfillan, Vitale, McNutt, & McComb, 2016; Keller et al., 2003). For instance, rhesus monkeys (*Macaca mulatta*) looked longer when acoustic-visual stimuli are presented in an incongruent scenario (Sliwa, Duhamel, Pascalis, & Wirth, 2011). Most studies investigating individual recognition have primarily focused on the vocal domain using acoustical playback experiments. After displaying a call (e.g., combination of calls from different individuals) from a hidden speaker, the researcher records the immediate behaviours of the subject(s) and compares the responses (e.g., looking time, approach/move away of the speaker) when the acoustic stimuli violate or fit its (their) expectations ('violation-of-expectation' paradigm: Baillargeon, 1987). This study design is a valuable method to reveal the content and the extent of social knowledge on wild and semi-wild populations.

The foundational work of Cheney and Seyfarth (1980) on mother-offspring recognition in vervet monkeys has provided an important framework for research on vocal individual recognition. Over the years, several studies have shown the unidirectional or mutual vocal recognition between kin or non-kin groupmates, mostly between mother and offspring in primate (Fischer, 2004; but see Simons & Bielert, 1973) and non-primate species (Balcombe &

McCracken, 1992; de la Torre, Briefer, Ochocki, McElligott, & Reader, 2016). Moreover, the presence of linear dominance relationships (Casey, Charrier, Mathevon, & Reichmuth, 2015; Reber, Townsend, Manser, & Manser, 2013) and social bond strength (Fedurek, Machanda, Schel, & Slocombe, 2013; Palombit, Seyfarth, & Cheney, 1997) provide other avenues to investigate the extent of social knowledge. As an illustration, Cheney and Seyfarth (1997) conducted playback experiments on female chacma baboons (*P. ursinus*) to test the effect of previous interactions on a subject's behaviours. They made use of the fact that after a fight, the aggressor (i.e., higher-ranking female) sometimes grunted while approaching her victim. When 'reconciliatory grunts' were simulated in the aftermath of a conflict, the victim looked longer toward the speaker when the opponent's grunts were played than when the grunts of another higher-ranking female were played. Moreover, the victim was more likely to approach her opponent after hearing her reconciliatory grunts. Therefore, female chacma baboons can compare their own social status with other conspecifics and are able to take into account recent interactions to draw inferences on the target of a vocalisation (see also Engh, Hoffmeier, Cheney, & Seyfarth, 2006; reviewed in Vasconcelos, 2008).

1.3.2. Knowledge about the relationships of others

Based on the accurate identification of individuals and their classification with an appropriate social label (**section 1.3.1.**), animals are able to track and memorise social relationships that groupmates have with one another without being directly involved (Cheney & Seyfarth, 2007; Tomasello & Call, 1997). Based on a non-egocentric viewpoint, animals monitor the social interactions of others to predict and adjust their behaviours according to recent events involving individuals other than themselves (e.g., transitive inference: Engh, Siebert, Greenberg, & Holekamp, 2005; Grosenick, Clement, & Fernald, 2007).

Experiments using matching-to-sample designs suggested that primates recognize kin relationships of third-parties based on pictures of mother-offspring pairs (Dasser, 1988; but see Vokey, Rendall, Tangen, Parr, & de Waal, 2004). Further strong evidence using playbacks (Cheney & Seyfarth, 1999; Wittig, Crockford, Wikberg, Seyfarth, & Cheney, 2007; Wittig et al., 2014) and behavioural observations (Judge, 1982; Tiddi, di Sorrentino, Fischer, & Schino, 2017) indicated that knowledge on other's kin relationships are not only restricted to mother-offspring dyads, but can extend to more distant kin, such as sibling and cousin.

Moreover, by using vocal sequences mimicking a rank reversal (i.e., threat-grunts of a subordinate female and scream of a dominant one), Cheney, Seyfarth and Silk (1995a) found that female chacma baboons are aware of the current dominance hierarchy among females of their troop (see also Borgeaud, van de Waal, & Bshary, 2013; Kitchen, Cheney, & Seyfarth, 2005). In

Cercopithecines, females of the same matriline generally share similar dominance rank, as they inherit the status from their mother (Cheney & Seyfarth, 1990). Based on this dominance pattern, a well design playback experiment simulating rank reversal within- or between-matriline showed that female chacma baboons distinguish dominance rank and kinship (Bergman, Beehner, Cheney, & Seyfarth, 2003). Consequently, it seems that female chacma baboons have a “concept” of others’ matrilineal kin and rank as two independent social entities (see also Schino, Tiddi, & Di Sorrentino, 2006).

While kinship can be stable over years, animals are also able to accurately track transient relationships among groupmates. For instance, in chacma baboons, high-ranking males of a group have prior access to swelling female, as mating success is correlated with the dominance rank (Weingrill, Lycett, & Henzi, 2000). Until the end of the female swelling, they form a “sexual consortship” characterised by guarding the female from any approaching males. To assess whether male chacma baboons monitor other’s sexual relationships (i.e., “sexual consortship”: Seyfarth, 1976b), Crockford and her colleagues (2007) performed a playback experiment using two loudspeakers separated one from the other. In the trial condition (i.e., simulating the end of the consortship), one speaker played the grunts from a male directly followed by the copulation call of his consort swelling female from a second speaker. Male chacma baboons, particularly subordinate males, responded strongly to sequences where the consort pair’ calls were displayed from different speakers. Indeed, they associate those two spatially separate calls as a break-up of the consortship pair and, consequently, as a potential opportunity to mate with this female (i.e., “sneaky” copulation). Thus, this experiment suggests that males in this despotic species track mating relationships of other group mates and use this transient and unpredictable information to maximize their own mating success. However, a similar playback design revealed that bachelor male geladas (*Theropithecus gelada*) — a closely related species of the baboon genus — lack interest toward incongruent acoustic sequences simulating a copulation between a unit male and a female of different units (Le Roux & Bergman, 2012), even though bachelor males are responsible for female takeover, frequently followed by infanticide of the unit male’s unweaned offspring (Beehner & Bergman, 2008).

Finally, previous studies have shown that bystanders can interfere in the grooming interactions of other conspecifics, by aggressing the dyad or placing themselves in between the grooming partners (Mondragón-Ceballos, 2001; Schino & Lasio, 2018; but see Kummer, Bachmann, Abegglen, Falett, & Sigg, 1978). This third-party intervention highlight that animals keep track of differentiated third-party relationships in terms of social bond strength, independently of the kinship (Tiddi et al., 2017). Knowing “who is friend with whom” is a relevant information as it can negatively affect bystanders. For instance, the quality of a bonded pair is correlated with the dominance status in ravens (*Corvus corax*: Massen, Szapl, & Spreafico,

2014). Therefore, bystanders might benefit from monitoring this social information, as bonded pairs can prevent the formation of a new one, and potentially prevent rank reversal.

In sum, animals including primates utilise the wide variety of information heard in vocalisations, such as the identity of the caller, context of emission and past interactions, to inform their decisions. Moreover, animals are able to monitor the direct and indirect relationships with or among others to optimally adapt their behaviours to a particular individual and/or situation. As a result, receivers of these vocalisations may profit from the acquisition of those social knowledge and use them strategically, for example to choose which partners to support during agonistic confrontations (Berghänel, Ostner, & Schülke, 2011; Gilby et al., 2013). Vocalisations also allow victims to avoid social interaction or proximity with a member of the aggressor's kin, limiting the risk of receiving kin-biased redirected aggression (Cheney & Seyfarth, 1999). This suggests that beyond learning individual traits and acquiring third-party knowledge, primates are able to create indirect causal relations between events that are temporally and spatially distant (e.g., agonistic interaction followed by reconciliatory behaviours: Wittig et al., 2014, 2007). However, the contrasting results observed in gelada and chacma baboon males raise the question whether the social system might influence the motivation to monitor others' relationships (see **Chapter 3**).

1.4. The peculiar case of the West African baboons

The six phenotypically distinct baboon species — *P. anubis*, *P. cynocephalus*, *P. hamadryas*, *P. kindae*, *P. papio* and *P. ursinus* — have a highly variable group size, sex ratio, social structure and mating system, even sometimes between populations of the same species (Barrett & Henzi, 2008). Baboons live in a wide variety of ecological conditions across the African continent and in the Arabian Peninsula, across which predation risks and food availability differ significantly (Barrett & Henzi, 2008). Moreover, active hybridisation zones have been recorded when interspecific home ranges overlap, evidently affecting behaviours, social organisation, genetic and life history of the offspring that are produced (e.g., Jolly, Burrell, Phillips-Conroy, Bergey, & Rogers, 2011; Zinner, Arnold, & Roos, 2011). Thus, baboons represent an interesting model to study how ecological factors and population variations influence the characteristics of their societies (Barrett & Henzi, 2008; Jolly, 2009) and therefore their social cognition.

Similarly to the societies of hamadryas baboons (Schreier & Swedell, 2009) and geladas (Dunbar, 1984), Guinea baboons (*P. papio*) live in a complex multi-level social system divided in different sub-structures (Patzelt et al., 2014; Patzelt et al., 2011). The smaller entity of their group is called a 'unit' (i.e., 'primary male', 1-6 females and their offspring, and 'secondary males') representing the core of their society (reviewed in Fischer et al., 2017). Those subgroups

aggregate to form a stable ‘party’ and two-three parties form sometimes a ‘gang’ during fusion phases, e.g., while travelling (Patzelt et al., 2014). Genetic evidence suggests that females disperse between parties and gangs, whereas males are usually philopatric (Kopp et al., 2014; Kopp, Fischer, Patzelt, Roos, & Zinner, 2015), although male transfers have been observed (Faraut, personal observation). How female Guinea baboons decide to transfer and select their mate is still unclear. Generally, it is suggested that female dispersal is a strategy to avoid endogamy, to increase the reproductive success and/or to reduce the competition for mates or resources (Perrin & Mazalov, 2000). Females transferring with offspring may also reduce the risk of infanticide (Teichroeb, Wikberg, & Sicotte, 2009). This last hypothesis, however, is unlikely to be a main selective pressure in Guinea baboons, as no infanticidal attack has been recorded in more than ten years of data collection (Fischer et al., 2017).

Mixed findings concerning the male-female association patterns in Guinea baboons (Boese, 1973, 1975; Galat-Luong, Galat, & Hagell, 2006; Maestriperieri, Mayhew, Carlson, Hoffman, & Radtke, 2007; Sharman, 1982) led Goffe and her colleagues (2016) to investigate the intersexual social relationships. Their results showed that one to six females present in the unit can be spatially distant from their associated adult male, called “primary” male. Males, however, do not appear to spatially segregate their mates like hamadryas baboons, possibly because in diverse primate species mate guarding is costly, disturbs normal foraging activity (Alberts, Altmann, & Wilson, 1996) and increases glucocorticoid levels (Girard-Buttoz et al., 2014). Even if the majority of social behaviours (i.e., affiliation, aggression, greeting and copulation) are directed toward the primary male, females do not receive aggression when they interact with others, so called ‘secondary’ males. Females are rarely observed copulating with other males than their primary male (Goffe, Zinner, & Fischer, 2016; Maestriperieri, Leoni, Raza, Hirsch, & Whitham, 2005) and recent paternity analysis confirmed that the primary male sired most of the offspring within its unit (89.5%: Dal Pesco, Trede, Zinner, & Fischer, in prep). Thus, females take an active role in the maintenance of the mating relationships and can remain several years with the same primary male (Goffe et al., 2016). Notably, female Guinea baboons sometimes counter-aggress and form coalitions against their primary males (Goffe et al., 2016; Kalbitzer, Heistermann, Cheney, Seyfarth, & Fischer, 2015), a behaviour also recorded in geladas (Dunbar, 1984).

Since the early report of Boese (1973), authors have been surprised by the relatively low level of competition characterising Guinea baboon male-male relationships, especially the noticeable high spatial tolerance across the different social levels (Patzelt et al., 2014; Patzelt et al., 2011) or the rare instance of aggressions recorded (Kalbitzer et al., 2015). Indeed, several unsuccessful attempts have been made to detect a linear dominance hierarchy (Dal Pesco et al., in prep; Kalbitzer et al., 2015; Patzelt et al., 2014). Furthermore, a previous playback experiment

suggested that Guinea baboon males looked longer toward the speaker when a male's grunts of their own gang was displayed than when they heard neighbouring or stranger males' vocalisations (Maciej, Patzelt, Ndao, Hammerschmidt, & Fischer, 2013). This low interest toward grunts from out-group males lies in sharp contrast with the previous works in other primate species (e.g., Kitchen et al., 2005; Range, 2005), as generally out-group males can jeopardize the safety of the group (e.g., Beehner & Bergman, 2008; Collins, Busse, & Goodall, 1984). Male philopatry could be the main driver of this relaxed social structure among male Guinea baboons (Jolly, 2009; Patzelt et al., 2014). Although males exchange an extensive amount of ritualised greeting interactions without constraining them to their preferential partners (Dal Pesco & Fischer, 2018), grooming interactions and coalition formations are almost exclusively exchanged between preferential partners, even after reaching sexual maturity (Dal Pesco et al., in prep; Galat-Luong et al., 2006; Kalbitzer et al., 2015; Patzelt et al., 2014). However, male relatedness is not a precondition for the formation of high relationship strength (Dal Pesco et al., in prep). Interestingly, those preferential relationships can be maintained over several years, but do not seem to increase the reproductive benefits of the males (Dal Pesco et al., in prep). Overall, the relaxed relationships characterising male-female and male-male interactions set the Guinea baboon apart from other *Papio* species.

1.5. Aim and approaches

The principal motivation of this PhD thesis was to determine whether differing social systems can impact the vocal usage and/or the allocation of social attention by investigating a wild population of Guinea baboons. As the grunt is considered the most frequently uttered vocalisation in Cercopithecines (and even beyond: Laporte & Zuberbühler, 2010; Nogueira, Caselli, Costa, Moura, & Nogueira-Filho, 2016; Pflüger & Fichtel, 2012), I investigated its usage when emitted by an individual approaching a groupmate. I conducted playback experiments using this close-proximity vocalisation to assess whether male Guinea baboons monitor the social relationships of male-female associations.

The first objective of this PhD was to investigate the function of grunts during approaches in the tolerant Guinea baboons (**Chapter 2**). Here, I built on previous work investigating the function of this vocalisation in various primate species but, I incorporated all possible sex combinations of subject-partner dyads separately. Despite having a similar acoustic structure to other baboon species, call usage in Guinea baboons appears to be different from closely related species (e.g., copulation and loud calls: Maciej, Ndao, Hammerschmidt, & Fischer, 2013). I examined whether the nature of post-approach interactions during behavioural focal observations was modulated by the grunt production of the approaching individual.

Subsequently, I tested how the quality of relationships between interacting partners and infant presence influence the grunt utterance.

The second part of this thesis (**Chapter 3**) explored the third-party knowledge of adult male Guinea baboons. As males seem to possess some degree of vocal recognition (see Maciej, Patzelt, et al., 2013), I performed playback experiments to assess if they track the current pattern of male-female associations within their own party. To accomplish this, I established whether grunts occurred more frequently between individuals of the same unit or from different units during behavioural focal observations. Then, I created congruent and incongruent acoustic sequences simulating an interaction between a female and a primary male from the same or from different units respectively.

In a general discussion (**Chapter 4**), I summarize the main results of those studies and integrate them into a broader comparative framework. I finally propose outlooks for future avenues of research within this domain.

CHAPTER 2 - How life in a tolerant society affects the usage of grunts: Evidence from male and female Guinea baboons

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CHAPTER 3 - How life in a tolerant society affects the attention to social information in baboons

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CHAPTER 4 – General discussion

In this dissertation, I revealed that the peculiar social system characterising the Guinea baboon society acts on their vocal usage and the attention allocated to others' interactions. This thesis provides a valuable contribution to the knowledge on the evolution of signalling and cognition within the sub-tribe *Papionina*. Also, the results shed light on the social pressures associated with living in complex groups and which aspects of social systems could shape signalling and cognition in baboons and geladas.

In this general discussion, I will give a brief overview over the main findings on grunt usage (**section 4.1.**) and the response to grunts from usual and unusual context in Guinea baboons (**section 4.2.**). I will further evaluate the effects of social complexity on communicative systems, cognition and brain (**section 4.3.**), make suggestions about future promising lines of research (**section 4.4.**), and end with some concluding remarks (**section 4.5.**).

4.1. Function and usage of grunts

In corroboration with previous findings in other species, grunts in Guinea baboons signal the benign intent of the approaching animal to engage in peaceful interactions with the partner (i.e., grooming, contact sitting) or the partner's infant (i.e., gentle manipulation). In addition, grunts are used strategically according to the uncertainty of the subject-partner relationship (Silk et al., 2000). Indeed, the probability of Guinea baboon females to utter grunts decreased when bond strength increased. Moreover, males were more likely to utter grunts while approaching a female with an infant in close-proximity, a pattern also recorded in male chacma baboons (Palombit, Cheney, & Seyfarth, 1999).




Nevertheless, interspecific differences emerged regarding some aspects of relationships on grunt utterance. First, the subject-partner bond strength in female Guinea baboons impacted their grunt production only in presence of an infant with her partner. This result suggests that females vocalise to mollify their partner rather than to express their internal state. Unfortunately, it was not possible to compare this result with other studies investigating grunt usage in female dyads, as the interaction between bond strength and infant presence was not analysed in chacma baboons (Silk et al., 2016), and the impact of female bond strength in olive baboons was not tested statistically (Silk et al., 2018). Second, the absence of a dominance effect on the utterance of grunts between females could be related to the overall low rate of displacement and physical aggressions in Guinea baboons. However, the rate of agonistic interactions in the more despotic olive and chacma baboons was not reported (Silk et al., 2018, 2016), prohibiting the phylogenetic comparisons between different baboon species. Third, I did not detect a significant effect of the

strength of bonds between males and across heterosexual dyads on grunt usage, a result in line with the relaxed social structure both within and between sexes in Guinea baboons. Indeed, males maintain high spatial tolerance (Fischer et al., 2017) and even engage in intense ritualized greeting interactions with each other (Dal Pesco & Fischer, 2018). Moreover, primary males tolerate their associated females to affiliate with secondary males and to access to monopolised food resources such as meat (Goffe & Fischer, 2016). Why sexually mature male Guinea baboons do not form rank relationships according to a linear dominance hierarchy is, however, puzzling. Kalbitzer and his colleagues (2015) proposed that the lack of competition over mating partners and the formation of strong social bonds (Dal Pesco et al., in prep) explain the low rate of aggressions and the lack of clear dominance hierarchy among male Guinea baboons (see summarising **Table 5.1**).

Genetic constraints limit the structure and extent of vocal repertoire within taxa and, therefore, variations in social systems between baboons have minor impacts on the vocal structure (Hammerschmidt & Fischer, 2019). However, the contexts in which grunts and other vocalisations are given can vary among baboons. For instance, male loud calls (“wahoos”) are given in foraging and travelling contexts in Guinea baboons, whereas chacma baboon males use them during aggressive displays (Maciej, Ndao, et al., 2013; Fischer et al., 2004; Kitchen, Seyfarth, Fischer, & Cheney, 2003; see also “coos” and “gruffs” in macaques: Owren, Dieter, Seyfarth, & Cheney, 1993). The frequency in which each call is given can also vary. Considering the proportion of ‘vocal approaches’ toward a female (i.e., approach associated with grunts), olive baboon females grunted in 12% (Silk et al., 2018), Guinea baboon females in 22%, and female chacma baboons vocalize in 28% of all approaches (Silk et al., 2016). Moreover, female Guinea baboons do not systematically vocalise during copulation (60% of all copulatory acts: Faraut, personal observation), and patterns of vocalisations in the mating context vary markedly across baboon species (56% in *P. kinda*: Petersdorf, personal communication; 61% in *P. anubis*: Bouquet et al., 2018; 97% in *P. ursinus*: O’Connell & Cowlshaw, 1994; 97% in *P. cynocephalus*: Semple, McComb, Alberts, & Altmann, 2002). By examining the function and usage of an affiliative vocalisation in Guinea baboons (**Chapter 2**), our observations support the assumption that the degree of social uncertainty and tolerance shape the context of call usage, even in non-competitive or non-sexual situations.

Table 5.1

Features of the social system, grunt usage and male social knowledge in the four compared *Papionina* species.

	 Chacma baboon	 Olive baboon	 Guinea baboon	 Gelada
Male dominance Infanticide Female takeover	Strict Yes Yes ¹	Strict Rare Yes ²	Unclear No No ⁴	Unclear Yes Yes ³
Philopatric sex	Female ⁵	Female ⁵	Mainly male ⁴	Female ⁶
Mating system	Polygynandrous ⁷	Polygynandrous ²	Polygyny-monandrous ⁴	Polygyny-monandrous ⁸
Female dominance	Matrilineal ⁵	Matrilineal ⁵	Within and between unit ⁹	Matrilineal ⁶
Post-approach interactions when grunt uttered	Dyads ♀♀: ↑ infant handling and affiliation ↓ aggression and displacement ¹⁰	Dyads ♀♀: ↑ infant handling and affiliation ↓ aggression Longer proximity ¹¹	All dyads: ↑ infant handling and affiliation ↓ displacement ⁹	n/a (but see ¹²)
Factors affecting grunt usage	Dyads ♀♀: Infant presence Relative rank Kinship ¹⁰ Dyads ♂♀: ♀ reproductive state ¹⁰	Dyads ♀♀: Infant presence Relative rank DSI and kinship ¹¹ Dyads ♂♀: n/a	Dyads ♀♀: Infant presence Unit membership DSI (when infant) ⁹ Dyads ♂♀: Infant presence ⁹	n/a
♂ triadic knowledge	♂-♀ association and ♂ dominance ¹³	n/a	♂-♀ association ¹⁸	No tracking of ♂-♀ association ¹⁶
♂ dyadic knowledge	“Friend” (♀) ¹⁴	“Friend” (♀) ¹⁵	Residency status (♂) ¹⁹	No tracking of group membership (♂) ¹⁷

n/a: no data available; ♀: female; ♂: male; DSI: Dyadic Social Index. Photo credits: L. Faraut, U. Kalbitzer, F.M.D. Paciência

¹Weingrill (2000); ²Henzi & Barrett (2003) ; ³Beehner & Bergman (2008); Snyder-Mackler, Alberts, & Bergman (2012); ⁴Fischer et al. (2017); ⁵Altmann & Alberts (2003); ⁶Le Roux, Beehner, & Bergman (2011); ⁷Seyfarth (1976); ⁸Johnson, Snyder-Mackler, Lu, Bergman, & Beehner (2018); ⁹**Chapter 2**; ¹⁰Palombit et al. (1999); Silk et al. (2016); ¹¹Silk et al. (2018); ¹²Aich, Moos-Heilen, & Zimmermann (1990); ¹³Crockford et al. (2007); Kitchen et al. (2005); ¹⁴Palombit et al. (1997); ¹⁵Lemasson et al. (2008); ¹⁶Le Roux & Bergman (2012); ¹⁷Bergman (2010); ¹⁸**Chapter 3**; ¹⁹Maciej, Patzelt, et al. (2013).

4.2. Social knowledge and monitoring of others' interactions

In our study population, a previous playback experiment provided evidence that adult male Guinea baboons are able to recognise the residency status of other males based on their grunts (Maciej, Patzelt, et al., 2013). Specifically, males were highly interested in grunts produced by members of their own gang in comparison to neighbouring and stranger males. Yet, their orienting reactions could be explained by the broad “familiar-stranger” categorisation of individuals, a discriminatory skill widespread among animals (Tibbetts & Dale, 2007; Wiley, 2013). Further, as indicated by my results (**Chapter 3**), males are capable of distinguishing conspecifics based on individually acoustic features of their grunts (Owren, Seyfarth, & Cheney, 1997; Rendall, 2003). Therefore, one could argue that our subjects showed “true individual recognition” based on audible interactions of others (see definition by Tibbetts & Dale, 2007). Moreover, the scope of their social knowledge ranges beyond the unit level (i.e., core of their society: Fischer et al., 2017). This indicates that male Guinea baboons are highly attentive to unit membership and possess accurate knowledge of their social surroundings. By using grunts in playback experiments, we could additionally show that affiliative vocalisation can be a salient stimulus similarly to copulation calls or screams used in previous playback experiments (e.g., Crockford et al., 2007; Lemasson et al., 2008).

In line with other playback experiments on the closely related chacma baboons (Crockford et al., 2007), Guinea baboon males can differentiate between consistent or unusual mate associations, indicating that they accurately monitor the current unit association of their own party. However, it is important to stress that unit association in Guinea baboons can be stable over a long period of time (up to four years: Faraut, personal observation), whereas chacma baboon males form temporary associations with females (i.e., duration of the oestrus: Seyfarth, 1976). Considering the unexpected higher interest toward congruent male-female associations — and grunts from males of their own gang (Maciej, Patzelt, et al., 2013) —, familiarity might represent a more valuable information in Guinea baboon males, a bias previously reported in other species while considering the looking duration toward familiar or unfamiliar faces of conspecifics (Park et al., 2010; Somppi et al., 2014). Thus, my playback experiments add to the existing evidence that the value allocated to social information is highly dependent on the mating system and the level of despotism of a society (see summarising **Table 5.1**).

Our findings in male Guinea baboons contrast the lack of orienting responses observed in male geladas, who seem to have limited individual vocal recognition regarding group members outside their own “unit” or their bachelor group (Bergman, 2010; Le Roux & Bergman, 2012). An alternative explanation could be that male geladas simply lack motivation to keep track of

interactions between partners outside their unit. Similar to Guinea baboons, unit male geladas can tolerate spatial overlap with other units (Snyder-Mackler et al., 2012a). Moreover, adult bachelor males exchange a high rate of grooming interactions (Pappano, 2013). Taking into account the similarities between Guinea baboons and geladas, social factors other than mating system and the level of male competition could have driven the lack of behavioural responses observed in the playback experiments on geladas. Their social organisation is also characterised by a multi-level society, with the unit representing the lowest social level (Dunbar & Dunbar, 1975; Snyder-Mackler, Beehner, & Bergman, 2012) — and potentially the smallest cognitive entities (Bergman, 2010). Indeed, geladas are highly gregarious animals (mean “group” size: 16 individuals; range: 13-1000 individuals: Snyder-Mackler et al., 2012b) and extremely “chatty” (Johnson, 2018). Therefore, monitoring all acoustic interactions can become challenging, and geladas might simply not be motivated to process all information, especially in the almost perpetual din. An important point that needs to be taken into account is the level of social complexity in these two species. Indeed, numerous differentiated relationships (metric provided by Bergman & Beehner, 2015) exist across different levels of the Guinea baboon society: coalitions (personal observation) and ritualised greetings occur between males of different parties (Dal Pesco & Fischer, 2018), secondary males can be affiliated to different units (Dal Pesco et al., in prep) and females form bonds even between units (Goffe, 2016). Geladas, on the other hand, interact with a more restricted number of conspecifics, as affiliative interactions occur exclusively within the unit (Johnson, Snyder-Mackler, Beehner, & Bergman, 2014) or between preferential partners in the bachelor group (Pappano, 2013). Consequently, the diversity of relationships observed in Guinea baboons versus geladas might be an appropriate social factor predicting variations in cognitive abilities (i.e., social knowledge).

4.3. Exploring the impacts of social complexity

4.3.1. Communication

With regard to communication, some authors argued that egalitarian social systems, where social relationships are uncertain (e.g., more counter-aggression, no clear dominance hierarchy), could be more demanding than despotic societies, where dominance hierarchies and kinship severely determine the pattern of interactions (Freeberg, Dunbar, & Ord, 2012). As a result, tolerant societies might present a greater communicative complexity in terms of behavioural repertoire size and graded variations among signals. This statement supports the “Social Complexity hypothesis for communicative complexity”, referring to the intertwined association between the degree of complexity of communicative systems and social interactions (Freeberg et al., 2012). Even if the call structure does not differ despite the difference in social

systems (Hammerschmidt & Fischer, 2019), the variations of vocal usage (**Chapter 2**) observed between the different species of baboons support this hypothesis. For instance, dominance status and social bonds are highly dependent on kinship in female chacma and olive baboons (Altmann & Alberts, 2003), and represent two important predictors of grunt utterance (Silk et al., 2018, 2016). On the other hand, unit membership and social bonds, more likely to fluctuate over time, explain most of the variations of grunt usage in female Guinea baboons.

Interspecific variations in the context of signal usage are not only restricted to vocal behaviours. Indeed, comparative work in macaques made reference to the constraints of “social style” (Thierry, 2007) on the diversity and the flexibility of gestural and facial repertoires, mostly in the affiliative contexts (reviewed in Dobson, 2012). For example, the use of “teeth chattering” (see definition by van Hooff, 1967) by the relatively tolerant Barbary macaques (*Macaca sylvanus*) occurs across different contexts, i.e., submission, appeasement, affiliation and reassurance (Wiper & Semple, 2007), whereas in the more despotic rhesus macaques (*M. mulatta*), this facial expression is relatively rare and essentially displayed up the dominance hierarchy (i.e., submission: Maestriperri, 2007). Although macaque is also a good model to test the effect of variation of social structure on communicative systems, the four levels of tolerance defined by Thierry (2007) are essentially based on female data, making comparisons impossible while considering male behaviours.

While egalitarian/despotic social structure drives or limits the evolution of communicative systems, other social aspects, such as group size (May-Collado, Agnarsson, & Wartzok, 2007), care system (Leighton, 2017) and mating system (Stirling & Thomas, 2003), have been proposed to explain variations in the complexity of signalling modalities (auditory, visual and olfactory) between species of the same phylogenetic group (reviewed by Peckre, Kappeler, & Fichtel, 2019). However, the underlying mechanisms as well as the direction of causality remains uncertain, whether the social complexity emerged as a result or as a consequence of the richness and variability of communicative systems, or whether they co-evolved (Freeberg et al., 2012; Gustison, Johnson, Bergman, & Beehner, 2019).

4.3.2. Cognition

Similar to the communicative systems, cognitive processes are not uniform across closely related species and seem to arise from a higher degree of social complexity. Despite the close degree of relatedness and substantial ecological similarities between Guinea and chacma baboons (Barrett & Henzi, 2008; Fischer et al., 2017), the differing demands of social lifestyle (e.g., degree of male-male competition/tolerance) seem to explain the differences in the attention allocated to third-party information, but not their social knowledge, as males of both species discriminate

consistent versus inconsistent male-female associations (Crockford et al., 2007; **Chapter 3**). In gelada males, the restricted amount of differentiated relationships and the considerably large group size combined with constant vocal inputs might represent a cognitive cost affecting the content of their social knowledge or their motivation to keep track of triadic interactions (Bergman, 2010; Le Roux & Bergman, 2012). Supporting the Social Intelligence (Social Brain or Social Complexity) hypothesis (e.g., Barton & Dunbar, 1997), the results of those playback experiments corroborate with the growing body of research, postulating that cognition can be enhanced by the different dimensions of complex societies. As an illustration, the level of social tolerance (on cooperative task: Hare et al., 2007), the level of fission-fusion (on inhibitory control: Amici et al., 2008), or group-living versus solitary species (on transitive inference: MacLean, Merritt, & Brannon, 2008) appear to be important social factors affecting both the social and physical cognition in primates. Moreover, a recent comparative analysis among four species of macaques with different social styles revealed a strong effect of social tolerance on socio-cognitive tasks (e.g., inhibitory control), whereas the performance of those species were equivalent in the physical domain (Joly et al., 2017). Those results reveal domain-specific cognitive performances undergone by selective evolutionary pressures across species in response to specific social and non-social challenges (see also Amici, Barney, Johnson, Call, & Aureli, 2012). As a result, different species can outperformed others in one task, but not another (Amici et al., 2012). However, the results of Joly and her co-workers' comparative investigation should be considered carefully, as only females were tested in one species (*M. fascicularis*), the degree of tolerance in macaques is based on female behaviours (Thierry, 2007) and the social partner was a human experiment and not another conspecific.

As mentioned previously, the Social Intelligence hypothesis was extensively tested in the primate lineage. However, there is now compelling comparative evidence that other non-primate mammal taxa (e.g., *Panthera* sp. and spotted hyena, *Crocuta crocuta*: Borrego & Gaines, 2016; bottlenose dolphin, *Tursiops* sp.: Connor, Sherwin, & Kru, 2012) and some bird species (e.g., jay sp.: Bond, Kamil, & Balda, 2003; parrot sp.: Krashenninnikova, Braeger, & Wanker, 2013), possess sophisticated cognitive skills that fluctuate according to the complexity of their social systems. To some extents, evolutionary convergence across species from different taxa appears to emerge when animals face similar social challenges leading to similar cognitive adaptations (Emery & Clayton, 2004).

4.3.3. Brain activity and structures

Presumably, social complexity may have exerted important pressures on specific brain structures regarding the neuronal bases responsible for communication and social cognition.

Indeed, the adequate and rapid encoding of others' behaviours, and the constant regulation of the response represent selective pressures in the evolution of primate brain (Dunbar & Shultz, 2007b). Consequently, the presentation of stimuli carrying valuable social information can influence primate brain activity. Indeed, the firing rate of the neurons in the lateral intraparietal area mirrored rhesus macaque's preferences towards pictures of female hindquarters and dominant male faces versus subordinate male faces (Klein, Deaner, & Platt, 2008). In addition, neuronal plasticity in specific brain structures (e.g., amygdala and anterior cingulate cortex in rhesus macaque; caudal nidopallium and hippocampal complex in zebra finch, *Taeniopygia guttata*) has been detected when the animals were transferred into larger social groups (Barnea, Mishal, & Nottebohm, 2006; Sallet et al., 2011). The authors suggested that those neural extensions might be essential for the ability to appropriately decode the exponential amount of information generated by bigger social network. Similarly, evidence showed that the dominance status of rhesus macaques is correlated with important modifications of six particular brain regions, such as the raphe nucleus and amygdala (Noonan et al., 2014; Sallet et al., 2011).

However, the main source of knowledge in social neurosciences often comes from an extremely limited variety of stimuli — mainly aggressive or neutral expressions (Ghazanfar & Santos, 2004) — and a restricted diversity of species are used as models to explain brain processes. Although this approach opens a window into the underlying mechanisms of animal mind, it neglects species-typical social behaviours (Ghazanfar & Santos, 2004). In his book *The Evolution of Communication*, Hauser (1996, p. 610) concluded that: “[...] brains exhibit design features suited to solve socioecologically meaningful problems”. Therefore, replicating neuroanatomical and neurofunctional studies with more diverse stimuli and with selectively chosen species facing different selective pressures linked to their social environment is therefore fundamental, but can be a major challenge considering the ethical limitations of highly informative invasive procedures.

4.4. Future directions

Altogether, the results of my dissertation provide new insights into the vocal behaviour and social cognition of the tolerant Guinea baboons and propose several directions for future research in a natural setting regarding the different levels of potential social complexity (i.e., social organisation, mating system, social structure) governing the context of vocal utterance and the content of social knowledge.

4.4.1. Grunt usage

One remaining question is to what extent kinship affects the occurrence of grunts and other social behaviours. Indeed, Silk and her co-workers (2016, 2018) demonstrated that mother-

daughter dyads were less likely to grunt to each other during approaches (versus other kin and non-kin dyads). Furthermore, kinship typically plays a major role in the pattern of interactions and the strength of social bonds associated with long-term benefits (Silk et al., 2010, 2003). In male Guinea baboons, a recent study shows that kinship is not a precondition for the formation of preferential relationships (Dal Pesco et al., in prep). Even if preliminary results indicate that relatedness is not the main predictor of social patterns between female Guinea baboons (N = 15: Goffe, 2016), further genetic analyses are needed to fully understand the social structure of this species and subsequently the impact of kinship and social structure on communication.

To follow up on **Chapter 2**, future investigations in Guinea baboons could test whether affiliative vocal strategies can help to manage conflicts across different sex combinations. For instance, female chacma baboons use grunt as reconciliatory behaviour without systematically engaging in affiliative tactile interactions (Cheney et al., 1995b; Silk, 2002) and male geladas give preferentially long and complex vocal responses rather than affiliative behaviours to resolve agonistic encounters (Gustison, 2017). Given the low rate of aggressions recorded in Guinea baboon on a daily basis, additional data are required to investigate this question further.

To my knowledge, this is the first study investigating grunt usage among males independently of the other sex combinations. Even though we did not detect an effect of male social bonds, comparative analyses could reveal how grunt production functions between preferential males in other primate species, such as bachelor geladas (Pappano, 2013). Another avenue of research would be to investigate the ontogeny of grunt usage, for example do juvenile males used strategically this vocalization to develop social bonds with other male conspecifics.

4.4.2. Social knowledge

The presence of individual vocal recognition and the capacity to classify and monitor third-party associations detected in our study open doors for further investigations on the value allocated to intersexual interactions in Guinea baboons. We know from previous observations that female Guinea baboons transfer mainly to units of already established primary males (Goffe et al., 2016). Thus, the next step would be to explore to which extent males tolerate their female unit members to interact with other males, by creating sequences simulating a vocal interaction between the subject bonded female and another primary male. As primary males tolerate their females to affiliate with secondary males (Goffe et al., 2016), this paradigm could be used as a control grunt sequence. Playing the same simulated interactions (see **Chapter 3**), a second series of experiments could determine at which life-history stage males start to show interest and keep track of male-female associations by testing the third-party knowledge of subadults. Furthermore, as some species can recognise conspecifics' calls from neighbouring groups (e.g., Cheney &

Seyfarth, 1982), future studies could displayed female-male grunt sequences (used in **Chapter 3**) from a particular party to males of a different party to assess the extent of male social knowledge beyond the party level (i.e., from the same or a different gang). Furthermore, playback experiments with social stimuli of different values (e.g., scream versus grunt) for the unit male geladas would be essential to disentangle whether they focus selectively their attention toward vocal interactions of valuable partners (e.g., their own unit females) or they have limited vocal recognition as suggested by Bergman (2010).

Besides baboons and geladas, social knowledge and the salience of social information must be extended to other closely related species showing variations in their social systems, in order to confirm the impact of social complexity on social cognition (e.g., social structures in macaques: Thierry, 2007). Thus, another line of inquiry aims at exploring how individuals can subtly allocate their social attention toward preferential partners of the same sex. Given that enduring relationships and coalition formations among preferential male partners remain relatively rare in the animal kingdom (e.g., *M. sylvanus*: Berghänel et al., 2011; *Pan troglodytes*: Mitani, 2009; *Tursiops aduncus*: Möller et al., 2014; *M. nemestria*: Schülke et al., 2010), Guinea baboon or some macaque species would represent great models to test the impact of male bonds on social knowledge. For example, playback sequences could simulate an agonistic encounter involving at least one preferential partner or none (e.g., a threat-grunt of the male A followed by a distress scream of the male B; see Wittig et al., 2014).

Finally, extensive work examined both the content and the extent of female chacma baboons' knowledge, mainly in agonistic situations (e.g., Cheney & Seyfarth, 1997; Cheney et al., 1995a; Cheney & Seyfarth, 1999; Engh et al., 2006). As both spotted hyenas (Benson-Amram, Heinen, Dryer, & Holekamp, 2011; Tilson, Ronald & Hamilton, 1984) and African elephants (*Loxodonta africana*: Archie, Morrison, Foley, Moss, & Alberts, 2006; McComb, Moss, Sayialel, & Baker, 2000) live in female-bonded societies and possess sophisticated cognitive abilities like chacma baboons, these species are perfect non-primate models for testing the effect of dominance on female social knowledge to corroborate the results of chacma baboon females.

4.5. General conclusions

Exploring vocal communication offers a glimpse into the social cognition of our closest relatives. Combining behavioural observations and playback designs, I was able to increase our understanding about Guinea baboon social knowledge and further investigate the grunt usage in this tolerant species. In my project, I demonstrate that both males and females use grunts strategically to attenuate potential uncertainty in a post-approach situation. However, the female dominance hierarchy and the bond strength among heterosexual and male-male dyads were not

good predictors of grunt utterance in this species, reflecting their low competition level recorded. In addition, my second study revealed that Guinea baboons can identify individuals *via* vocal signals and tested the content of their social knowledge in a non-competitive social context. Those playback experiments showed that Guinea baboon males had surprisingly higher interest for familiar acoustic stimuli, consistent with the current patterns of associations.

Overall, the interspecific variations observed in the usage of calls and the motivation to accurately monitor third-party interactions are likely to be related to specific features of the social system. In agreement with the Social Intelligence hypothesis, the results of our studies contribute to our understanding of the adaptive values of communication and cognition necessary to face the challenging fluctuations of the social environment. Future research investigating communication and cognition should agree on reliable definitions of behaviours to avoid discrepancies between studies (e.g., what is an approach?). Furthermore, they should consider a set of measures to reveal how the competition, cohesion and/or cooperation respectively modulate the evolution of certain traits. As social relationships can vary over time, it would be relevant to use dynamic measures to infer the change of relationships and their impact on communication and social cognition. As a result, it will be easier to capture adequately which specific dimensions of animal sociality selectively pressure behaviours (e.g., signal usage), cognition (i.e., social and/or physical domain), and potentially brain structures (e.g., neural plasticity). Finally, extensive phylogenetic comparative investigations on carefully chosen species or populations (e.g., intra- versus intersexual interaction) differing in some dimensions of their social system are encouraged, as the social environment of many animal species seems to account for more variation than phylogenetic relatedness.

REFERENCES

- Aich, H., Moos-Heilen, R., & Zimmermann, E. (1990). Vocalizations of Adult Gelada Baboons (*Theropithecus gelada*): Acoustic Structure and Behavioural Context. *Folia Primatologica*, *55*, 109–132. <https://doi.org/10.1159/000156508>
- Albers, P. C. H., & de Vries, H. (2001). Elo-rating as a tool in the sequential estimation of dominance strengths. *Animal Behaviour*, *61*(2), 489–495. <https://doi.org/10.1006/anbe.2000.1571>
- Alberts, S. C., Altmann, J., & Wilson, M. L. (1996). Mate guarding constrains foraging activity of male baboons. *Animal Behaviour*, *51*, 1269–1277. <https://doi.org/10.1006/anbe.1996.0131>
- Altmann, J., & Alberts, S. C. (2003). Variability in reproductive success viewed from a life-history perspective in baboons. *American Journal of Human Biology*, *15*(3), 401–409. <https://doi.org/10.1002/ajhb.10157>
- Amici, F., Aureli, F., & Call, J. (2008). Fission-fusion dynamics, behavioral flexibility, and inhibitory control in primates. *Current Biology*, *18*, 1415–1419. <https://doi.org/10.1016/j.cub.2008.08.020>
- Amici, F., Barney, B., Johnson, V. E., Call, J., & Aureli, F. (2012). A Modular Mind? A Test Using Individual Data from Seven Primate Species. *PloS One*, *7*(12), 51918. <https://doi.org/10.1371/journal.pone.0051918>
- Archie, E. A., Moss, C. J., & Alberts, S. C. (2006). The ties that bind: genetic relatedness predicts the fission and fusion of social groups in wild African elephants. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1586), 513–522. <https://doi.org/10.1098/rspb.2005.3361>
- Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., ... Van Schaik, C. P. (2008). Fission-Fusion Dynamics: New Research Frameworks. *Current Anthropology*, *49*(4), 627–654. <https://doi.org/10.1086/586708>
- Axelrod, R. (1981). *The evolution of cooperation*. New York: Basic Book, Inc.
- Baillargeon, R. (1987). Object Permanence in 3 1/2- and 4 1/2-month-old infants. *Developmental Psychology*, *23*(5), 655–664. <https://doi.org/10.1037/0012-1649.23.5.655>
- Balcombe, J. P., & McCracken, G. F. (1992). Vocal recognition in Mexican free-tailed bats: do pups recognize mothers? *Animal Behaviour*, *43*(1), 79–87. [https://doi.org/10.1016/S0003-3472\(05\)80073-9](https://doi.org/10.1016/S0003-3472(05)80073-9)

- Barnea, A., Mishal, A., & Nottebohm, F. (2006). Social and spatial changes induce multiple survival regimes for new neurons in two regions of the adult brain: An anatomical representation of time? *Behavioural Brain Research*, *167*, 63–74.
<https://doi.org/10.1016/j.bbr.2005.08.018>
- Barrett, L., & Henzi, S. P. (2008). Baboons. *Current Biology: CB*, *18*(10), R404-6.
<https://doi.org/10.1016/j.cub.2008.02.074>
- Barton, R. A., & Dunbar, R. I. M. (1997). Evolution of the social brain. In R. W. Byrne & A. Whiten (Eds.), *Machiavellian intelligence II: Extensions and Evaluations* (p. 405). St. Andrews: Cambridge University Press.
- Beehner, J. C., & Bergman, T. J. (2008). Infant mortality following male takeovers in wild geladas. *American Journal of Primatology*, *70*(12), 1152–1159. <https://doi.org/10.1002/ajp.20614>
- Benson-Amram, S., Dantzer, B., Stricker, G., Swanson, E. M., & Holekamp, K. E. (2016). Brain size predicts problem-solving ability in mammalian carnivores. *Proceedings of the National Academy of Sciences*, *113*(9), 2532–2537. <https://doi.org/10.1073/pnas.1505913113>
- Benson-Amram, S., Heinen, V. K., Dryer, S. L., & Holekamp, K. E. (2011). Numerical assessment and individual call discrimination by wild spotted hyenas, *Crocuta crocuta*. *Animal Behaviour*, *82*(4), 743–752. <https://doi.org/10.1016/j.anbehav.2011.07.004>
- Bercovitch, F. B., Hauser, D., & Jones, J. H. (1995). The endocrine stress response and alarm vocalizations in rhesus macaques. *Animal Behaviour*, *49*(2), 1703–1706.
- Berghänel, A., Ostner, J., & Schülke, O. (2011). Coalitions destabilize dyadic dominance relationships in male Barbary macaques (*Macaca sylvanus*). *Behaviour*, *148*(11), 1256–1274.
<https://doi.org/10.1163/000579511X600628>
- Bergman, T. J. (2010). Experimental evidence for limited vocal recognition in a wild primate: implications for the social complexity hypothesis. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1696), 3045–3053. <https://doi.org/10.1098/rspb.2010.0580>
- Bergman, T. J., & Beehner, J. C. (2015). Measuring social complexity. *Animal Behaviour*, *103*, 203–209. <https://doi.org/10.1016/j.anbehav.2015.02.018>
- Bergman, T. J., Beehner, J. C., Cheney, D. L., & Seyfarth, R. M. (2003). Hierarchical classification by rank and kinship in baboons. *Science*, *302*(5648), 1234–1236.
<https://doi.org/10.1126/science.1087513>

- Bergman, T. J., & Sheehan, M. J. (2013). Social knowledge and signals in primates. *American Journal of Primatology*, 75(7), 683–694. <https://doi.org/10.1002/ajp.22103>
- Boese, G. K. (1973). *Behavior and Social Organization of the Guinea Baboon (Papio papio)*. School of Hygiene and Public Health. Johns Hopkins University.
- Boese, G. K. (1975). Social behavior and ecological considerations of West African baboons (Papio papio). In R. H. Tuttle (Ed.), *Socioecology and Psychology of Primates* (pp. 205–230). Mouton: The Hague.
- Bond, A. B., Kamil, A. C., & Balda, R. P. (2003). Social complexity and transitive inference in corvids. *Animal Behaviour*, 65(3), 479–487. <https://doi.org/http://dx.doi.org/10.1006/anbe.2003.2101>
- Borgeaud, C., Schneider, A., Krützen, M., & Bshary, R. (2017). Female vervet monkeys fine-tune decisions on tolerance versus conflict in a communication network. *Proceedings of the Royal Society B: Biological Sciences*, 284, 19–22. <https://doi.org/10.1098/rspb.2017.1922>
- Borgeaud, C., van de Waal, E., & Bshary, R. (2013). Third-Party Ranks Knowledge in Wild Vervet Monkeys (*Chlorocebus aethiops pygerythrus*). *PLoS ONE*, 8(3), 8–11. <https://doi.org/10.1371/journal.pone.0058562>
- Borjon, J. I., Takahashi, D. Y., Cervantes, D. C., & Ghazanfar, A. A. (2016). Arousal dynamics drive vocal production in marmoset monkeys. *Journal of Neurophysiology*, 116(2), 753–764. <https://doi.org/10.1152/jn.00136.2016>
- Borrego, N., & Gaines, M. (2016). Social carnivores outperform asocial carnivores on an innovative problem. *Animal Behaviour*, 114, 21–26. <https://doi.org/10.1016/j.anbehav.2016.01.013>
- Bouquet, Y., Stephan, C., Johnson, C. A., Rothman, J. M., Neumann, C., & Zuberbühler, K. (2018). Comparing functions of copulation calls in wild olive baboons, *Papio anubis*, using multimodel inference. *Animal Behaviour*, 135, 187–197. <https://doi.org/10.1016/j.anbehav.2017.11.019>
- Boyer, D., & Ramos-Fernández, G. (2018). Contribution of social network analysis and collective phenomena to understanding social complexity and cognition. In *Evolution of Primate Social Cognition* (pp. 111–127). Cham: Springer.
- Briefer, E. F. (2012). Vocal expression of emotions in mammals: Mechanisms of production and

- evidence. *Journal of Zoology*, 288(1), 1–20. <https://doi.org/10.1111/j.1469-7998.2012.00920.x>
- Briseno-Jaramillo, M., Ramos-Fernández, G., Palacios-Romo, T. M., Sosa-López, J. R., & Lemasson, A. (2018). Age and social affinity effects on contact call interactions in free-ranging spider monkeys. *Behavioral Ecology and Sociobiology*, 72, 192. <https://doi.org/10.1007/s00265-018-2615-2>
- Brown, M., & Waser, P. M. (2018). Group movements in response to competitors' calls indicate conflicts of interest between male and female grey-cheeked mangabeys. *American Journal of Primatology*, (October 2017), e22918. <https://doi.org/10.1002/ajp.22918>
- Brumm, H., & Zollinger, S. A. (2011). The evolution of the Lombard effect : 100 years of psychoacoustic research. *Behaviour*, 148, 1173–1198. <https://doi.org/10.1163/000579511X605759>
- Byrne, R. W., & Whiten, A. (1988). *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans*. (R. W. Byrne & A. Whiten, Eds.) (Oxford, UK). Oxford University Press.
- Casey, C., Charrier, I., Mathevon, N., & Reichmuth, C. (2015). Rival assessment among northern elephant seals: evidence of associative learning during male–male contests. *Royal Society Open Science*, 2, 150228. <https://doi.org/10.1098/rsos.150228>
- Cheney, D. L., & Seyfarth, R. M. (1980). Vocal recognition in free-ranging vervet monkeys. *Animal Behaviour*, 28(2), 362–367. [https://doi.org/10.1016/S0003-3472\(80\)80044-3](https://doi.org/10.1016/S0003-3472(80)80044-3)
- Cheney, D. L., & Seyfarth, R. M. (1982). Recognition of Individuals within and between Groups of Free-Ranging Vervet Monkeys. *American Zoologist*, 22(22), 519–529. Retrieved from <http://www.jstor.org/stable/3882575>
<http://www.jstor.org/stable/3882575>
<http://www.jstor.org/stable/3882575>
- Cheney, D. L., & Seyfarth, R. M. (1985). Social and Non-Social Knowledge in Vervet Monkeys. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 308(1135), 187–201. <https://doi.org/10.1098/rstb.1985.0019>
- Cheney, D. L., & Seyfarth, R. M. (1985). Vervet Monkey Alarm Calls: Manipulation Through Shared Information? *Behaviour*, 94(1), 150–166. <https://doi.org/10.1163/156853985X00316>
- Cheney, D. L., & Seyfarth, R. M. (1990). *How monkeys see the world*. University of Chicago Press.

- Cheney, D. L., & Seyfarth, R. M. (1997). Reconciliatory grunts by dominant female baboons influence victims' behaviour. *Animal Behaviour*, *54*(2), 409–18. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/9268473>
- Cheney, D. L., & Seyfarth, R. M. (1999). Recognition of other individuals' social relationships by female baboons. *Animal Behaviour*, *58*(1), 67–75. <https://doi.org/10.1006/anbe.1999.1131>
- Cheney, D. L., & Seyfarth, R. M. (2007). *Baboon metaphysics: The Evolution of a Social Mind*. Chicago: University of Chicago Press.
- Cheney, D. L., Seyfarth, R. M., & Silk, J. B. (1995a). The responses of female baboons (*Papio cynocephalus ursinus*) to anomalous social interactions: evidence for causal reasoning? *Journal of Comparative Psychology*, *109*(2), 134–141. <https://doi.org/10.1037//0735-7036.109.2.134>
- Cheney, D. L., Seyfarth, R. M., & Silk, J. B. (1995b). The role of grunts in reconciling opponents and facilitating interactions among adult female baboons. *Animal Behaviour*, *50*(1), 249–257. <https://doi.org/10.1006/anbe.1995.0237>
- Cheney, D., & Seyfarth, R. (1990). Attending to behaviour versus attending to knowledge: examining monkeys' attribution of mental states. *Animal Behaviour*, *40*(4), 742–753. [https://doi.org/10.1016/S0003-3472\(05\)80703-1](https://doi.org/10.1016/S0003-3472(05)80703-1)
- Clay, Z., Smith, C. L., & Blumstein, D. T. (2012). Food-associated vocalizations in mammals and birds: what do these calls really mean? *Animal Behaviour*, *83*(2), 323–330. <https://doi.org/10.1016/j.anbehav.2011.12.008>
- Collier, K., Radford, A. N., Townsend, S. W., & Manser, M. B. (2017). Wild dwarf mongooses produce general alert and predator-specific alarm calls. *Behavioral Ecology*, *28*(5), 1293–1301. <https://doi.org/10.1093/beheco/arx091>
- Collins, D., Busse, C., & Goodall, J. (1984). Infanticide in two populations of savannah baboons. In G. Hausfater & S. B. Hrdy (Eds.), *Infanticide: a comparative and evolutionary perspective*. (pp. 193–215). New York: Aldine.
- Connor, R. C., Sherwin, W. B., & Kru, M. (2012). A novel mammalian social structure in Indo-Pacific bottlenose dolphins (*Tursiops* sp.): complex male alliances in an open social network. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1740), rspb20120264. <https://doi.org/10.1098/rspb.2012.0264>
- Connor, R. C., Smolker, R. A., & Richards, A. F. (1992). Two levels of alliance formation among

- male bottlenose dolphins (*Tursiops* sp.). *Journal of Evolutionary Biology*, 5(3), 523–528.
<https://doi.org/10.1046/j.1420-9101.1992.5030523.x>
- Cowl, V. B., & Shultz, S. (2017). Large brains and groups associated with high rates of agonism in primates. *Behavioral Ecology*, 28(3), 803–810. <https://doi.org/10.1093/beheco/axx041>
- Crockford, C., Wittig, R. M., Seyfarth, R. M., & Cheney, D. L. (2007). Baboons eavesdrop to deduce mating opportunities. *Animal Behaviour*, 73(5), 885–890.
<https://doi.org/10.1016/j.anbehav.2006.10.016>
- Dal Pesco, F., & Fischer, J. (2018). Greetings in male Guinea baboons and the function of rituals in complex social groups. *Journal of Human Evolution*, 125, 87–98.
<https://doi.org/10.1016/j.jhevol.2018.10.007>
- Dal Pesco, F., Trede, F., Zinner, D., & Fischer, J. (n.d.). Fitness benefits of male-male sociality in wild Guinea baboons (*Papio papio*), in prep.
- Dasser, V. (1988). A social concept in Java monkeys. *Animal Behaviour*, 36, 225–230.
[https://doi.org/10.1016/S0003-3472\(88\)80265-3](https://doi.org/10.1016/S0003-3472(88)80265-3)
- Dawkins, R., & Krebs, J. R. (1978). Animal signals: information or manipulation. In K. JR & N. B. Davies (Eds.), *Behavioural ecology: An evolutionary approach* (Vol. 2, pp. 292–309). Oxford: Blackwell.
- de la Torre, M. P., Briefer, E. F., Ochocki, B. M., McElligott, A. G., & Reader, T. (2016). Mother-offspring recognition via contact calls in cattle (*Bos taurus*). *Animal Behaviour*, 114, 147–154.
<https://doi.org/doi.org/10.1016/j.anbehav.2016.02.004>
- Dobson, S. D. (2012). Coevolution of Facial Expression and Social Tolerance in Macaques. *American Journal of Primatology*, 74(3), 229–235. <https://doi.org/10.1002/ajp.21991>
- Dunbar, R. I. M. (1984). *Reproductive decisions: An economic analysis of gelada baboon social strategies*. Princeton University Press.
- Dunbar, R. I. M. (1992). Neocortex size as a constraint on group size in primates. *Journal of Human Evolution*, 22(6), 469–493. [https://doi.org/10.1016/0047-2484\(92\)90081-J](https://doi.org/10.1016/0047-2484(92)90081-J)
- Dunbar, R. I. M. (1998). The Social Brain Hypothesis. *Evolutionary Anthropology*, 178–190.
[https://doi.org/10.1002/\(SICI\)1520-6505\(1998\)6:5<178::AID-EVAN5>3.0.CO;2-8](https://doi.org/10.1002/(SICI)1520-6505(1998)6:5<178::AID-EVAN5>3.0.CO;2-8)
- Dunbar, R. I. M., & Dunbar, P. (1975). Social dynamics of gelada baboons. *Contribution to*

Primate, 6, 175.

Dunbar, R. I. M., & Shultz, S. (2007a). Evolution in the social brain. *Science*, 317, 1344–1347.
<https://doi.org/10.1126/science.1145463>

Dunbar, R. I. M., & Shultz, S. (2007b). Understanding primate brain evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362(1480), 649–658.
<https://doi.org/10.1098/rstb.2006.2001>

Dyble, M., Thompson, J., Smith, D., Vinicuis, L., Mace, R., Migliano, A. B., ... Migliano, A. B. (2017). Networks of Food Sharing Reveal the Functional Significance of Multilevel Sociality in Two Hunter-Report Networks of Food Sharing Reveal the Functional Significance of Multilevel Sociality in Two Hunter-Gatherer Groups. *Current Biology*, 26(15), 2017–2021.
<https://doi.org/10.1016/j.cub.2016.05.064>

Egnor, S. E. R., Wickelgren, J. G., & Hauser, M. D. (2007). Tracking silence: Adjusting vocal production to avoid acoustic interference. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 193(4), 477–483. <https://doi.org/10.1007/s00359-006-0205-7>

Emery, N. J., & Clayton, N. S. (2004). The mentality of crows: convergent evolution of intelligence in corvids and apes. *Science*, 306(5703), 1903–7.
<https://doi.org/10.1126/science.1098410>

Engh, A. L., Hoffmeier, R. R., Cheney, D. L., & Seyfarth, R. M. (2006). Who, me? Can baboons infer the target of vocalizations? *Animal Behaviour*, 71(2), 381–387.
<https://doi.org/10.1016/j.anbehav.2005.05.009>

Engh, A. L., Siebert, E. R., Greenberg, D. A., & Holekamp, K. E. (2005). Patterns of alliance formation and postconflict aggression indicate spotted hyaenas recognize third-party relationships. *Animal Behaviour*, 69(1), 209–217.
<https://doi.org/10.1016/j.anbehav.2004.04.013>

Ey, E., Hammerschmidt, K., Seyfarth, R. M., & Fischer, J. (2007). Age- and sex-related variations in clear calls of *Papio ursinus*. *International Journal of Primatology*, 28(4), 947–960.
<https://doi.org/10.1007/s10764-007-9139-3>

Ey, E., Rahn, C., Hammerschmidt, K., & Fischer, J. (2009). Wild female olive baboons adapt their grunt vocalizations to environmental conditions. *Ethology*, 115(5), 493–503.

- <https://doi.org/10.1111/j.1439-0310.2009.01638.x>
- Fedurek, P., Machanda, Z. P., Schel, A. M., & Slocombe, K. E. (2013). Pant hoot chorusing and social bonds in male chimpanzees. *Animal Behaviour*, *86*(1), 189–196.
<https://doi.org/10.1016/j.anbehav.2013.05.010>
- Fichtel, C., & Van Schaik, C. P. (2006). Semantic differences in sifaka (*Propithecus verreauxi*) alarm calls: A reflection of genetic or cultural variants? *Ethology*, *112*(9), 839–849.
<https://doi.org/10.1111/j.1439-0310.2006.01239.x>
- Fischer, J. (2004). Emergence of individual recognition in young macaques. *Animal Behaviour*, *67*(4), 655–661. <https://doi.org/10.1016/j.anbehav.2003.08.006>
- Fischer, J. (2011). Where Is the Information in Animal Communication? *Animal Thinking: Contemporary Issues in Comparative Cognition*, *8*, 151–161.
<https://doi.org/10.7551/mitpress/9780262016636.003.0010>
- Fischer, J., Farnworth, M. S., Sennhenn-Reulen, H., & Hammerschmidt, K. (2017). Quantifying social complexity. *Animal Behaviour*, *130*, 57–66.
<https://doi.org/10.1016/j.anbehav.2017.06.003>
- Fischer, J., Kitchen, D. M., Seyfarth, R. M., & Cheney, D. L. (2004). Baboon loud calls advertise male quality: acoustic features and their relation to rank, age, and exhaustion. *Behavioral Ecology and Sociobiology*, *56*(2), 140–148. <https://doi.org/10.1007/s00265-003-0739-4>
- Fischer, J., Kopp, G. H., Dal Pesco, F., Goffe, A., Hammerschmidt, K., Kalbitzer, U., ... Zinner, D. (2017). Charting the neglected West: The social system of Guinea baboons. *American Journal of Physical Anthropology*, *162*(63), 15–31. <https://doi.org/10.1002/ajpa.23144>
- Fischer, J., & Price, T. (2017). Meaning, intention, and inference in primate vocal communication. *Neuroscience and Biobehavioral Reviews*, *3*(3), 1602838.
<https://doi.org/10.1016/j.neubiorev.2016.10.014>
- Fischer, J., Wheeler, B. C., & Higham, J. P. (2015). Is there any evidence for vocal learning in chimpanzee food calls? *Current Biology: CB*, *25*(21), R1028–R1029.
<https://doi.org/10.1016/j.cub.2015.09.010>
- Fischer, J., & Zinner, D. (2011). Communication and cognition in primate group movement. *International Journal of Primatology*, *32*(6), 1279–1295. <https://doi.org/10.1007/s10764-011-9542-7>

- Fitch, W. T. (2010). *The Evolution of Language*. New York: Cambridge University Press.
- Freeberg, T. M., Dunbar, R. I. M., & Ord, T. J. (2012). Social complexity as a proximate and ultimate factor in communicative complexity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1597), 1785–1801. <https://doi.org/10.1098/rstb.2011.0213>
- Galat-Luong, A., Galat, G., & Hagell, S. (2006). The social and ecological flexibility of Guinea baboons: implications for Guinea baboon social organization and male strategies. In L. Swedell & S. R. Leigh (Eds.), *Reproduction and Fitness in Baboons: Behavioral, Ecological, and Life History Perspectives Developments in Primatology: Progress and Prospects* (pp. 105–121). Springer. <https://doi.org/10.1007/978-0-387-33674-9>
- Gall, G. E. C., & Manser, M. B. (2017). Group cohesion in foraging meerkats: follow the moving “vocal hot spot.” *Royal Society Open Science*, 4, 170004. <https://doi.org/10.1098/rsos.170004>
- Geissmann, T. (1984). Inheritance of song parameters in the gibbon song, analysed in two hybrid gibbons (*Hylobates pileatus* X *H. lar*). *Folia Primatologica*, 42, 216–235. <https://doi.org/10.1159/000156165>
- Ghazanfar, A. A., & Santos, L. R. (2004). Primate brains in the wild: The sensory bases for social interactions. *Nature Reviews Neuroscience*, 5(8), 603–616. <https://doi.org/10.1038/nrn1473>
- Gilby, I. C., Brent, L. J. N., Wroblewski, E. E., Rudicell, R. S., Hahn, B. H., Goodall, J., & Pusey, A. E. (2013). Fitness benefits of coalitionary aggression in male chimpanzees. *Behavioral Ecology and Sociobiology*, 67(3), 373–381. <https://doi.org/10.1007/s00265-012-1457-6>
- Gilfillan, G., Vitale, J., McNutt, J. W., & McComb, K. (2016). Cross-modal individual recognition in wild African lions. *Biology Letters*, 12(8), 7–9. <https://doi.org/10.1098/rsbl.2016.0323>
- Girard-Buttoz, C., Heistermann, M., Rahmi, E., Agil, M., Ahmad Fauzan, P., & Engelhardt, A. (2014). Costs of mate-guarding in wild male long-tailed macaques (*Macaca fascicularis*): Physiological stress and aggression. *Hormones and Behavior*, 66(4), 637–648. <https://doi.org/10.1016/j.yhbeh.2014.09.003>
- Goffe, A. S. (2016). *Social relationships of female Guinea baboons (Papio papio) in Senegal*. (Thesis dissertation). Georg-August-Universität Göttingen.
- Goffe, A. S., & Fischer, J. (2016). Meat sharing between male and female Guinea baboons (*Papio papio*). *Primate Biology*, 3(1), 1–8. <https://doi.org/10.5194/pb-3-1-2016>

- Goffe, A. S., Zinner, D., & Fischer, J. (2016). Sex and friendship in a multilevel society: behavioural patterns and associations between female and male Guinea baboons. *Behavioral Ecology and Sociobiology*, *70*(3), 323–336. <https://doi.org/10.1007/s00265-015-2050-6>
- Grosenick, L., Clement, T. S., & Fernald, R. D. (2007). Fish can infer social rank by observation alone. *Nature*, *445*(7126), 429–432. <https://doi.org/https://doi.org/10.1038/nature05511>
- Gustison, M. L. (2017). *The phylogeny and function of vocal complexity in geladas*. (Thesis dissertation). University of Michigan.
- Gustison, M. L., Johnson, E. T., Bergman, T. J., & Beehner, J. C. (2019). The social functions of complex vocal sequences in wild geladas. *Behavioral Ecology and Sociobiology*, *73*(1), 14.
- Hage, S. R., Gavrilov, N., & Nieder, A. (2013). Cognitive control of distinct vocalizations in rhesus monkeys. *Journal of Cognitive Neuroscience*, *25*(10), 1692–1701. https://doi.org/10.1162/jocn_a_00428
- Hamilton, W. D. (1963). The Evolution of altruistic behavior. *The American Naturalist*, *97*(896), 354–356.
- Hammerschmidt, K., & Fischer, J. (2008). Constraints in primate vocal production. In U. Griebel & K. D. Oller (Eds.), *The evolution of communicative creativity: from fixed signals to contextual flexibility* (pp. 93–119). Cambridge: The MIT Press.
- Hammerschmidt, K., & Fischer, J. (2019). Baboon vocal repertoires and the evolution of primate vocal diversity. *Journal of Human Evolution*, *126*, 1–13. <https://doi.org/10.1016/j.jhevol.2018.10.010>
- Hare, B., Melis, A. P., Woods, V., Hastings, S., & Wrangham, R. (2007). Tolerance allows bonobos to outperform chimpanzees on a cooperative task. *Current Biology*, *17*(7), 619–623. <https://doi.org/10.1016/j.cub.2007.02.040>
- Hauser, M. (1996). *The evolution of communication*. Cambridge and London: MIT Press. <https://doi.org/10.1017/CBO9781107415324.004>
- Hauser, M. D., Teixidor, P., Fields, L., & Flaherty, R. (1993). Food-elicited calls in chimpanzees: Effects of food quantity and divisibility. *Animal Behaviour*, *45*(4), 817–819. <https://doi.org/10.1006/anbe.1993.1096>
- Healy, S. D., & Rowe, C. (2007). A critique of comparative studies of brain size. *Proceedings of the*

- Royal Society B: Biological Sciences*, 274(1609), 453–464.
<https://doi.org/10.1098/rspb.2006.3748>
- Henzi, P., & Barrett, L. (2003). Evolutionary ecology, sexual conflict, and behavioral differentiation among baboon populations. *Evolutionary Anthropology: Issues, News, and Reviews*, 12(5), 217–230. <https://doi.org/10.1002/evan.10121>
- Higham, J. P., Heistermann, M., Saggau, C., Agil, M., Perwitasari-Farajallah, D., & Engelhardt, A. (2012). Sexual signalling in female crested macaques and the evolution of primate fertility signals. *BMC Evolutionary Biology*, 12(1). <https://doi.org/10.1186/1471-2148-12-89>
- Hollén, L. I., & Radford, A. N. (2009). The development of alarm call behaviour in mammals and birds. *Animal Behaviour*, 78(4), 791–800. <https://doi.org/10.1016/j.anbehav.2009.07.021>
- Humphrey, N. K. (1976). The social function of intellect. In P. P. Bateson & R. A. Hinde (Eds.), *Growing points in ethology* (pp. 303–317). Cambridge, U.K: Cambridge University Press.
- Isler, K., & Van Schaik, C. P. (2006). Metabolic costs of brain size evolution. *Biology Letters*, 2(4), 557–560. <https://doi.org/10.1098/rsbl.2006.0538>
- Janik, V. M. (2014). Cetacean vocal learning and communication. *Current Opinion in Neurobiology*, 28, 60–65. <https://doi.org/10.1016/j.conb.2014.06.010>
- Janik, V. M., & Slater, P. J. B. (2000). The different roles of social learning in vocal communication. *Animal Behaviour*, 60(1), 1–11. <https://doi.org/10.1006/anbe.2000.1410>
- Jensen, K., Silk, J. B., Andrews, K., Bshary, R., Cheney, D. L., Emery, N., ... Teufel, C. (2011). Social knowledge. In *Animal Thinking: Contemporary Issues in Comparative Cognition* (pp. 267–290). Retrieved from <https://www.scopus.com/inward/record.uri?eid=2-s2.0-84894924889&partnerID=40&md5=a7d0d7893f8bf763998e9e2c96cc4929>
- Johnson, E. T. (2018). *Social and Ecological Challenges in Female Geladas: A Test of the Vocal Grooming Hypothesis*. (Thesis dissertation). University of Michigan.
- Johnson, E. T., Snyder-Mackler, N., Beehner, J. C., & Bergman, T. J. (2014). Kinship and Dominance Rank Influence the Strength of Social Bonds in Female Geladas (*Theropithecus gelada*). *International Journal of Primatology*, 35(1), 288–304. <https://doi.org/10.1007/s10764-013-9733-5>
- Johnson, E. T., Snyder-Mackler, N., Lu, A., Bergman, T. J., & Beehner, J. C. (2018). The

- Goldilocks Effect: Female geladas in mid-sized groups have higher fitness. *BioRxiv*, 348383.
<https://doi.org/10.1101/348383>
- Jolly, A. (1966). Lemur social behavior and primate intelligence. *Science*, *153*, 501–506.
<https://doi.org/10.1126/science.153.3735.501>
- Jolly, C. J. (2001). A Proper Study for Mankind : Analogies From the Papionin Monkeys and Their Implications for Human Evolution. *Yearbook of Physical Anthropology*, *204*, 177–204.
<https://doi.org/10.1002/ajpa.10021>
- Jolly, C. J. (2009). Fifty years of looking at Human evolution. *Current Anthropology*, *50*(2), 187–199.
<https://doi.org/10.1086/597196>
- Jolly, C. J., Burrell, A. S., Phillips-Conroy, J. E., Bergey, C., & Rogers, J. (2011). Kinda baboons (*Papio kindae*) and grayfoot chacma baboons (*P. ursinus griseipes*) hybridize in the Kafue river valley, Zambia. *American Journal of Primatology*, *73*(3), 291–303.
<https://doi.org/10.1002/ajp.20896>
- Joly, M., Micheletta, J., Langermans, J., Sterck, E. H., & Waller, B. (2017). Comparing physical and social cognitive skills in macaque species with different. *Proceedings of the Royal Society B: Biological Sciences*, *284*, 20162738. Retrieved from
[https://researchportal.port.ac.uk/portal/files/7563332/Joly_et_al_Proc_Roy_Soc_B_Post
Print_accepted_version.pdf](https://researchportal.port.ac.uk/portal/files/7563332/Joly_et_al_Proc_Roy_Soc_B_Post_Print_accepted_version.pdf)
- Judge, P. G. (1982). Redirection of aggression based on kinship in a captive group of pigtail macaques. *International Journal of Primatology*, *3*(3), 301. <https://doi.org/10.1007/BF02692263>
- Kalbitzer, U., Heistermann, M., Cheney, D., Seyfarth, R., & Fischer, J. (2015). Social behavior and patterns of testosterone and glucocorticoid levels differ between male chacma and Guinea baboons. *Hormones and Behavior*, *75*, 100–110.
<https://doi.org/10.1016/j.yhbeh.2015.08.013>
- Kappeler, P. M., & van Schaik, C. P. (2002). Evolution of Primate Social Systems. *International Journal of Primatology*, *23*(4), 707–740.
- Keller, M., Meurisse, M., Poindron, P., Nowak, R., Ferreira, G., Shayit, M., ... Lévy, F. (2003). Maternal experience influences the establishment of visual/auditory, but not olfactory recognition of the newborn lamb by ewes at parturition. *Developmental Psychobiology*, *43*(3), 167–176. <https://doi.org/10.1002/dev.10130>

- Kitchen, D. M. (2004). Alpha male black howler monkey responses to loud calls: Effect of numeric odds, male companion behaviour and reproductive investment. *Animal Behaviour*, *67*(1), 125–139. <https://doi.org/10.1016/j.anbehav.2003.03.007>
- Kitchen, D. M., Cheney, D. L., & Seyfarth, R. M. (2004). Factors mediating inter-group encounters in savannah baboons (*Papio cynocephalus ursinus*). *Behaviour*, *141*, 197–218.
- Kitchen, D. M., Cheney, D. L., & Seyfarth, R. M. (2005). Male chacma baboons (*Papio hamadryas ursinus*) discriminate loud call contests between rivals of different relative ranks. *Animal Cognition*, *8*(1), 1–6. <https://doi.org/10.1007/s10071-004-0222-2>
- Kitchen, D. M., Seyfarth, R. M., Fischer, J., & Cheney, D. L. (2003). Loud calls as indicators of dominance in male baboons (*Papio cynocephalus ursinus*). *Behavioral Ecology and Sociobiology*, *53*(6), 374–384. <https://doi.org/10.1007/s00265-003-0588-1>
- Klein, J. T., Deaner, R. O., & Platt, M. L. (2008). Neural correlates of social target value in macaque parietal cortex. *Current Biology*, *18*(6), 419–424. <https://doi.org/10.1016/j.cub.2008.02.047>
- Knörnschild, M., Nagy, M., Metz, M., Mayer, F., & Von Helversen, O. (2010). Complex vocal imitation during ontogeny in a bat. *Biology Letters*, *6*(2), 156–159. <https://doi.org/10.1098/rsbl.2009.0685>
- Kopp, G. H., Ferreira da Silva, M. J., Fischer, J., Brito, J. C., Regnaut, S., Roos, C., & Zinner, D. (2014). The Influence of Social Systems on Patterns of Mitochondrial DNA Variation in Baboons. *International Journal of Primatology*, *35*(1), 210–225. <https://doi.org/10.1007/s10764-013-9725-5>
- Kopp, G. H., Fischer, J., Patzelt, A., Roos, C., & Zinner, D. (2015). Population genetic insights into the social organization of Guinea baboons (*Papio papio*): Evidence for female-biased dispersal. *American Journal of Primatology*, *77*(8), 878–889. <https://doi.org/10.1002/ajp.22415>
- Krasheninnikova, A., Braeger, S., & Wanker, R. (2013). Means–end comprehension in four parrot species: explained by social complexity. *Animal Cognition*, *16*, 755–764. <https://doi.org/10.1007/s10071-013-0609-z>
- Kummer, H., Bachmann, C., Abegglen, J. J., Falett, J., & Sigg, H. (1978). Grooming relationship and object competition among hamadryas baboons. *Recent Advances in Primatology*, *1*, 31–38.
- Lameira, A. R., Hardus, M. E., Mielke, A., Wich, S. A., & Shumaker, R. W. (2016). Vocal fold

- control beyond the species-specific repertoire in an orang-utan. *Scientific Reports*, *6*, 1–10.
<https://doi.org/10.1038/srep30315>
- Laporte, M. N. C., & Zuberbühler, K. (2010). Vocal greeting behaviour in wild chimpanzee females. *Animal Behaviour*, *80*(3), 467–473. <https://doi.org/10.1016/j.anbehav.2010.06.005>
- Le Roux, A., Beehner, J. C., & Bergman, T. J. (2011). Female philopatry and dominance patterns in wild geladas. *American Journal of Primatology*, *73*(5), 422–430.
<https://doi.org/10.1002/ajp.20916>
- Le Roux, A., & Bergman, T. J. (2012). Indirect rival assessment in a social primate, *Theropithecus gelada*. *Animal Behaviour*, *83*(1), 249–255. <https://doi.org/10.1016/j.anbehav.2011.10.034>
- Le Roux, A., Snyder-Mackler, N., Roberts, E. K., Beehner, J. C., & Bergman, T. J. (2013). Evidence for tactical concealment in a wild primate. *Nature Communications*, *4*, 1462–1466.
<https://doi.org/10.1038/ncomms2468>
- Leighton, G. M. (2017). Cooperative breeding influences the number and type of vocalizations in avian lineages. *Proceedings of the Royal Society B: Biological Sciences*, *284*, 20171508.
<https://doi.org/10.1098/rspb.2017.1508>
- Lemasson, A., Palombit, R. A., & Jubin, R. (2008). Friendships between males and lactating females in a free-ranging group of olive baboons (*Papio hamadryas anubis*): evidence from playback experiments. *Behavioral Ecology and Sociobiology*, *62*, 1027–1035.
<https://doi.org/10.1007/s00265-007-0530-z>
- Lindenfors, P., Nunn, C. L., & Barton, R. A. (2007). Primate brain architecture and selection in relation to sex. *BMC Biology*, *5*(1), 20. <https://doi.org/10.1186/1741-7007-5-20>
- Maciej, P., Ndao, I., Hammerschmidt, K., & Fischer, J. (2013). Vocal communication in a complex multi-level society: constrained acoustic structure and flexible call usage in Guinea baboons. *Frontiers in Zoology*, *10*(1), 58. <https://doi.org/10.1186/1742-9994-10-58>
- Maciej, P., Patzelt, A., Ndao, I., Hammerschmidt, K., & Fischer, J. (2013). Social monitoring in a multilevel society: a playback study with male Guinea baboons. *Behavioral Ecology and Sociobiology*, *67*(1), 61–68. <https://doi.org/10.1007/s00265-012-1425-1>
- MacLean, E. L., Merritt, D. J., & Brannon, E. M. (2008). Social complexity predicts transitive reasoning in Prosimian primates. *Animal Behaviour*, *76*(2), 479–486.
<https://doi.org/10.1038/jid.2014.371>

- Maestripieri, D. (2005). On the importance of comparative research for the understanding of human behavior and development: A reply to Gottlieb & Lickliter (2004). *Social Development*, *14*(1), 181–186. <https://doi.org/10.1111/j.1467-9507.2005.00296.x>
- Maestripieri, D. (2007). Gestural communication in three species of macaques (*Macaca mulatta*, *M. nemestria*, *M. arctoides*): Use of signals in relation to dominance and social context. In K. Liebal, C. Müller, & S. Pika (Eds.), *Gestural Communication in Nonhuman and Human Primates* (John Benja, pp. 51–66). Amsterdam / Philadelphia.
- Maestripieri, D., Leoni, M., Raza, S. S., Hirsch, E. J., & Whitham, J. C. (2005). Female Copulation Calls in Guinea Baboons: Evidence for Postcopulatory Female Choice? *International Journal of Primatology*, *26*(4), 737–758. <https://doi.org/10.1007/s10764-005-5306-6>
- Maestripieri, D., Mayhew, J., Carlson, C. L., Hoffman, C. L., & Radtke, J. M. (2007). One-male harems and female social dynamics in Guinea baboons. *Folia Primatologica*, *78*(1), 56–68. <https://doi.org/10.1159/000095686>
- Manser, M. B., Seyfarth, R. M., & Cheney, D. L. (2002). Suricate alarm calls signal predator class and urgency. *Trends in Cognitive Sciences*, *6*(2), 2001–2003. [https://doi.org/10.1016/S1364-6613\(00\)01840-4](https://doi.org/10.1016/S1364-6613(00)01840-4)
- Marino, L., Sol, D., Toren, K., Lefebvre, L., Marino, L., & Sol, D. (2006). Does diving limit brain size in Cetaceans? *Marine Mammal Science*, *22*(2), 413–425. Retrieved from http://animalstudiesrepository.org/acwp_vsm
- Marler, P., Dufty, A., & Pickert, R. (1986). Vocal communication in the domestic chicken: I. Does a sender communicate information about the quality of a food referent to a receiver? *Animal Behaviour*, *34*(1), 188–193. [https://doi.org/10.1016/0003-3472\(86\)90022-9](https://doi.org/10.1016/0003-3472(86)90022-9)
- Masataka, N. (1983). Categorical responses to natural and synthesized alarm calls in Goeldi's monkeys (*Callimico goeldii*). *Primates*, *24*(1), 40–51. <https://doi.org/10.1007/BF02381452>
- Massen, J. J. M., Szapl, G., & Spreafico, M. (2014). Ravens Intervene in Others' Bonding Attempts. *Current Biology*, *24*(22), 2733–2736. <https://doi.org/10.1016/j.cub.2014.09.073>
- May-Collado, L. J., Agnarsson, I., & Wartzok, D. (2007). Phylogenetic review of tonal sound production in whales in relation to sociality. *BMC Evolutionary Biology*, *20*, 1–20. <https://doi.org/10.1186/1471-2148-7-136>
- Maynard Smith, J. M. (1978). Optimization theory in evolution. *Annual Review of Ecology and*

- Systematics*, 9(1), 31–56. <https://doi.org/10.1146/annurev.es.09.110178.000335>
- Mccomb, K., Moss, C., Sayialel, S., & Baker, L. (2000). Unusually extensive networks of vocal recognition in African elephants. *Animal Behaviour*, 59, 1103–1109. <https://doi.org/10.1006/anbe.2000.1406>
- McFarland, R., & Majolo, B. (2013). Coping with the cold: Predictors of survival in wild Barbary macaques, *Macaca sylvanus*. *Biology Letters*, 9(4), 20130428. <https://doi.org/10.1098/rsbl.2013.0428>
- McGregor, P. K., & Dabelsteen, J. (1996). Animal communication networks. In D. Kroodsma & E. Miller (Eds.), *Ecology and Evolution of Acoustic Communication in Birds* (pp. 409–425). Ithaca/NY: Cornell University Press.
- Miller, C. T., & Wang, X. (2006). Sensory-motor interactions modulate a primate vocal behavior: antiphonal calling in common marmosets. *Journal of Comparative Physiology A*, 192, 27–38. <https://doi.org/10.1007/s00359-005-0043-z>
- Mitani, J. C. (2009). Male chimpanzees form enduring and equitable social bonds. *Animal Behaviour*, 77(3), 633–640. <https://doi.org/10.1016/j.anbehav.2008.11.021>
- Mitani, J. C., Call, J., Kappeler, P. M., Palombit, R. A., & Silk, J. B. (2013). *The evolution of primate societies*. Chicago and London: The University of Chicago Press.
- Mitani, J. C., & Nishida, T. (1993). Contexts and social correlates of long-distance calling by male chimpanzees. *Animal Behaviour*. <https://doi.org/10.1163/1568539X-00003259>
- Möller, L. M., Beheregaray, L. B., Harcourt, R. G., Moller, L. M., Beheregaray, L. B., Harcourt, R. G., & Kriitzen, M. (2014). Alliance membership and kinship in wild male bottlenose dolphins (*Tursiops aduncus*) of southeastern Australia. *Proceedings of the Royal Society B: Biological Sciences*, 268(1479), 1941–1947. <https://doi.org/10.1098/rspb.2001.1756>
- Mondragón-Ceballos, R. (2001). Interfering in affiliations: sabotaging by stumptailed macaques, *Macaca arctoides*. *Animal Behaviour*, 62(6), 1179–1187.
- Morton, E. S., & Stutchbury, B. J. M. (2012). Vocal Communication in Androgynous Territorial Defense by Migratory Birds. *International Scholarly Research Network Zoology*, 2012. <https://doi.org/10.5402/2012/729307>
- Nogueira, S. S. C., Caselli, C. B., Costa, T. S. O., Moura, L. N., & Nogueira-Filho, S. L. G. (2016).

- The role of grunt calls in the social dominance hierarchy of the white-lipped peccary (*Mammalia, Tayassuidae*). *PLoS ONE*, *11*(7), 12–14.
<https://doi.org/10.1371/journal.pone.0158665>
- Noonan, M. P., Sallet, J., Mars, R. B., Neubert, F. X., O'Reilly, J. X., Andersson, J. L., ... Rushworth, M. F. S. (2014). A neural circuit covarying with social hierarchy in macaques. *PLoS Biology*, *12*(9), e1001940. <https://doi.org/10.1371/journal.pbio.1001940>
- O'Connell, S. M., & Cowlshaw, G. (1994). Infanticide avoidance, sperm competition and mate choice: the function of copulation calls in female baboons. *Animal Behaviour*, *48*, 687–694.
<https://doi.org/doi.org/10.1006/anbe.1994.1288>
- Overduin-de Vries, A. M., Olesen, C. U., de Vries, H., Spruijt, B. M., & Sterck, E. H. M. (2013). Sneak copulations in long-tailed macaques (*Macaca fascicularis*): No evidence for tactical deception. *Behavioral Ecology and Sociobiology*, *67*(1), 101–111.
<https://doi.org/10.1007/s00265-012-1430-4>
- Owren, M. J., Dieter, J. A., Seyfarth, R. M., & Cheney, D. L. (1993). Vocalizations of rhesus (*Macaca mulatta*) and Japanese (*M. Fuscata*) macaques cross-fostered between species show evidence of only limited modification. *Developmental Psychobiology*, *26*(7), 389–406.
<https://doi.org/10.1002/dev.420260703>
- Owren, M. J., Seyfarth, R. M., & Cheney, D. L. (1997). The acoustic features of vowel-like grunt calls in chacma baboons (*Papio cynocephalus ursinus*): implications for production processes and functions. *The Journal of the Acoustical Society of America*, *101*(5), 2951–2963.
<https://doi.org/10.1121/1.418523>
- Palombit, R. A., Cheney, D. L., & Seyfarth, R. M. (1999). Male grunts as mediator of social interaction with females in wild chacma baboons (*Papio cynocephalus ursinus*). *Behaviour*, *136*(2), 221–242. <https://doi.org/10.1163/156853999501298>
- Palombit, R. A., Seyfarth, R. M., & Cheney, D. L. (1997). The adaptive value of “friendships” to female baboons: experimental and observational evidence. *Animal Behaviour*, *54*, 599–614.
<https://doi.org/10.1006/anbe.1996.0457>
- Pappano, D. J. (2013). *The reproductive trajectories of bachelor geladas*. (Thesis dissertation). University of Michigan. <https://doi.org/10.1073/pnas.0703993104>
- Park, J., Shimojo, E., & Shimojo, S. (2010). Roles of familiarity and novelty in visual preference

- judgments are segregated across object categories. *Proceedings of the National Academy of Sciences*, 107(33), 14552–14555. <https://doi.org/10.1073/pnas.1004374107>
- Patzelt, A., Kopp, G. H., Ndao, I., Kalbitzer, U., Zinner, D., & Fischer, J. (2014). Male tolerance and male-male bonds in a multilevel primate society. *Proceedings of the National Academy of Sciences of the United States of America*, 1–6. <https://doi.org/10.1073/pnas.1405811111>
- Patzelt, A., Zinner, D., Fickenscher, G., Diedhiou, S., Camara, B., Stahl, D., & Fischer, J. (2011). Group Composition of Guinea Baboons (*Papio papio*) at a Water Place Suggests a Fluid Social Organization. *International Journal of Primatology*, 32(3), 652–668. <https://doi.org/10.1007/s10764-011-9493-z>
- Peckre, L. R., Kappeler, P. M., & Fichtel, C. (2019). Clarifying and expanding the social complexity hypothesis for communicative complexity. *Behavioral Ecology and Sociobiology*, 73(1), 11. <https://doi.org/10.1007/s00265-018-2605-4>
- Perrin, N., & Mazalov, V. (2000). Local competition, inbreeding, and the evolution of sex-biased dispersal. *The American Naturalist*, 155(1), 116–127. <https://doi.org/10.1086/303296>
- Pflüger, F. J., & Fichtel, C. (2012). On the function of redfronted lemur's close calls. *Animal Cognition*, 15(5), 823–831. <https://doi.org/10.1007/s10071-012-0507-9>
- Pollick, A. S., Gouzoules, H., & De Waal, F. B. M. (2005). Audience effects on food calls in captive brown capuchin monkeys, *Cebus apella*. *Animal Behaviour*, 70(6), 1273–1281. <https://doi.org/10.1016/j.anbehav.2005.03.007>
- Pradhan, G. R., Engelhardt, A., Van Schaik, C. P., & Maestriperi, D. (2006). The evolution of female copulation calls in primates: A review and a new model. *Behavioral Ecology and Sociobiology*, 59(3), 333–343. <https://doi.org/10.1007/s00265-005-0075-y>
- Radford, A. N. (2004). Vocal Coordination of Group Movement by Green Woodhoopoes (*Phoeniculus purpureus*). *Ethology*, 20, 11–20.
- Range, F. (2005). Female sooty mangabeys (*Cercocebus torquatus atys*) respond differently to males depending on the male's residence status—preliminary data. *American Journal of Primatology*, 65(4), 327–333. <https://doi.org/10.1002/ajp.20119>
- Reber, S. A., Townsend, S. W., Manser, M. B., & Manser, M. B. (2013). Social monitoring via close calls in meerkats. *Proceedings of the Royal Society B: Biological Sciences*, 280, 20131013.

- Rendall, D. (2003). Acoustic correlates of caller identity and affect intensity in the vowel-like grunt vocalizations of baboons. *The Journal of the Acoustical Society of America*, *113*(6), 3390. <https://doi.org/10.1121/1.1568942>
- Rendall, D., Seyfarth, R., Cheney, D., & Owren, M. (1999). The meaning and function of grunt variants in baboons. *Animal Behaviour*, *57*(3), 583–592. <https://doi.org/10.1006/anbe.1998.1031>
- Ruch, H., Zürcher, Y., & Burkart, J. M. (2018). The function and mechanism of vocal accommodation in humans and other primates. *Biological Reviews*, *93*(2), 996–1013. <https://doi.org/10.1111/brv.12382>
- Ryan, M. (1980). Female mate choice in a neotropical frog. *Science*, *209*(4455), 523–525. <https://doi.org/10.1126/science.209.4455.523>
- Sallet, J., Mars, R. B., Noonan, M. P., Andersson, J. L., O'Reilly, J. X., Jbabdi, S., ... Rushworth, M. F. S. (2011). Social network size affects neural circuits in macaques. *Science*, *334*(6056), 697–700.
- Schino, G., & Lasio, F. (2018). Competition for grooming partners and interference in affiliation among female mandrills. *Ethology*, *124*(8), 1–9. <https://doi.org/10.1111/eth.12763>
- Schino, G., Tiddi, B., & Di Sorrentino, E. P. (2006). Simultaneous classification by rank and kinship in Japanese macaques. *Animal Behaviour*, *71*(5), 1069–1074. <https://doi.org/10.1016/j.anbehav.2005.07.019>
- Schlenker, P., Chemla, E., Arnold, K., Lemasson, A., Ouattara, K., Stephan, C., ... Zuberbühler, K. (2014). Monkey semantics: Two “dialects” of Campbell’s monkey alarm calls. *Linguistics and Philosophy*, *37*(6), 439–501.
- Schreier, A. L., & Swedell, L. (2009). The fourth level of social structure in a multi-level society: ecological and social functions of clans in hamadryas baboons. *American Journal of Primatology*, *71*(11), 948–955. <https://doi.org/10.1002/ajp.20736>
- Schülke, O., Bhagavatula, J., Vigilant, L., & Ostner, J. (2010). Social bonds enhance reproductive success in male macaques. *Current Biology*, *20*(24), 2207–10. <https://doi.org/10.1016/j.cub.2010.10.058>
- Seagraves, K. M., Arthur, B. J., & Egnor, S. E. R. (2016). Evidence for an audience effect in mice: male social partners alter the male vocal response to female cues. *The Company of Biologists*,

- 219, 1437–1448. <https://doi.org/10.1242/jeb.129361>
- Semple, S., McComb, K., Alberts, S., & Altmann, J. (2002). Information content of female copulation calls in yellow baboons. *American Journal of Primatology*, *56*(1), 43–56. <https://doi.org/10.1002/ajp.1062>
- Seyfarth, R. (1976a). Social relationships among adult female baboons. *Animal Behaviour*, *24*(4), 917–938. [https://doi.org/10.1016/S0003-3472\(76\)80022-X](https://doi.org/10.1016/S0003-3472(76)80022-X)
- Seyfarth, R. M. (1976b). Social relationships among adult male and female baboons. I. Behaviours during sexual consortship. *Behaviour*, *64*(3–4), 204–226. <https://doi.org/10.1163/156853978X00035>
- Seyfarth, R. M., & Cheney, D. L. (2003). Meaning and emotion in animal vocalizations. In *Annals of the New York Academy of Sciences* (Vol. 1000, pp. 32–55). <https://doi.org/10.1196/annals.1280.004>
- Seyfarth, R. M., & Cheney, D. L. (2009). Seeing who we hear and hearing who we see. *Proceedings of the National Academy of Sciences*, *106*(3), 669–670. <https://doi.org/10.1037/vio0000055>
- Seyfarth, R. M., & Cheney, D. L. (2010). Production, usage, and comprehension in animal vocalizations. *Brain and Language*, *115*(1), 92–100. <https://doi.org/10.1016/j.bandl.2009.10.003>
- Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980). Vervet monkey alarm calls: Semantic communication in a free-ranging primate. *Animal Behaviour*, *28*(4), 1070–1094. [https://doi.org/10.1016/S0003-3472\(80\)80097-2](https://doi.org/10.1016/S0003-3472(80)80097-2)
- Sharman, M. J. (1982). *Feeding, ranging and social organisation of the Guinea baboon*. (Thesis dissertation). University of St Andrews.
- Shettleworth, S. J. (2010). *Cognition, Evolution, and Behavior* (2nd Ed., Vol. 39). Oxford: Oxford University Press.
- Silk, J. B. (2001). Grunts, Girneys, and Good Intentions: The Origins of Strategic Commitment in Nonhuman Primates. In R. Nesse (Ed.), *Evolution and the Capacity for Commitment* (pp. 138–157). Russell Sage Foundation.
- Silk, J. B. (2002). Kin selection in primate groups. *International Journal of Primatology*, *23*(4), 849–875. <https://doi.org/10.1023/A:1015581016205>

- Silk, J. B., Alberts, S. C., & Altmann, J. (2003). Social bonds of female baboons enhance infant survival. *Science*, *302*(5648), 1231–1234. <https://doi.org/10.1126/science.1088580>
- Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., ... Cheney, D. L. (2010). Female chacma baboons form strong, equitable, and enduring social bonds. *Behavioral Ecology and Sociobiology*, *64*(11), 1733–1747. <https://doi.org/10.1007/s00265-010-0986-0>
- Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., ... Cheney, D. L. (2010). Strong and consistent social bonds enhance the longevity of female baboons. *Current Biology*, *20*(15), 1359–1361. <https://doi.org/10.1016/j.cub.2010.05.067>
- Silk, J. B., Cheney, D., & Seyfarth, R. (2013). A practical guide to the study of social relationships. *Evolutionary Anthropology: Issues, News, and Reviews*, *22*(5), 213–225. <https://doi.org/10.1002/evan.21367>
- Silk, J. B., Kaldor, E., & Boyd, R. (2000). Cheap talk when interests conflict. *Animal Behaviour*, *59*(2), 423–432. <https://doi.org/10.1006/anbe.1999.1312>
- Silk, J. B., Rendall, D., Cheney, D. L., & Seyfarth, R. M. (2003). Natal attraction in adult female baboons (*Papio cynocephalus ursinus*) in the Moremi Reserve, Botswana. *Ethology*, *109*(8), 627–644. <https://doi.org/10.1046/j.1439-0310.2003.00907.x>
- Silk, J. B., Roberts, E. R., Städele, V., & Strum, S. C. (2018). To grunt or not to grunt: Factors governing call production in female olive baboons, *Papio anubis*. *Plos One*, *13*(11), e0204601. <https://doi.org/10.1371/journal.pone.0204601>
- Silk, J. B., Seyfarth, R. M., & Cheney, D. L. (2016). Strategic use of affiliative vocalizations by wild female baboons. *PLoS ONE*, *11*(10), 1–10. <https://doi.org/10.1371/journal.pone.0163978>
- Simons, R. C., & Bielert, C. F. (1973). An experimental study of vocal communication between mother and infant monkeys (*Macaca nemestrina*). *American Journal of Physical Anthropology*, *38*(2), 455–461. <https://doi.org/10.1002/ajpa.1330380248>
- Sliwa, J., Duhamel, J.-R., Pascalis, O., & Wirth, S. (2011). Spontaneous voice-face identity matching by rhesus monkeys for familiar conspecifics and humans. *Proceedings of the National Academy of Sciences*, *108*(4), 1735–1740. <https://doi.org/10.1073/pnas.1008169108>
- Slocombe, K. E., Kaller, T., Turman, L., Townsend, S. W., Papworth, S., Squibbs, P., &

- Zuberbühler, K. (2010). Production of food-associated calls in wild male chimpanzees is dependent on the composition of the audience. *Behavioral Ecology and Sociobiology*, *64*(12), 1959–1966. <https://doi.org/10.1007/s00265-010-1006-0>
- Snyder-Mackler, N., Alberts, S. C., & Bergman, T. J. (2012a). Concessions of an alpha male? Cooperative defence and shared reproduction in multi-male primate groups. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1743), 3788–3795. <https://doi.org/10.1098/rspb.2012.0842>
- Snyder-Mackler, N., Beehner, J. C., & Bergman, T. J. (2012b). Defining Higher Levels in the Multilevel Societies of Geladas (*Theropithecus gelada*). *International Journal of Primatology*, *33*(5), 1054–1068. <https://doi.org/10.1007/s10764-012-9584-5>
- Sol, D., Duncan, R. P., Blackburn, T. M., Cassey, P., & Lefebvre, L. (2005). Big brains, enhanced cognition, and response of birds to novel environments. *Proceedings of the National Academy of Sciences*, *102*(15), 5460–5465. <https://doi.org/10.1073/pnas.0408145102>
- Somppi, S., Törnqvist, H., Hänninen, L., Krause, C. M., & Vainio, O. (2014). How dogs scan familiar and inverted faces: An eye movement study. *Animal Cognition*, *17*(3), 793–803. <https://doi.org/10.1007/s10071-013-0713-0>
- Sperber, A. L., Werner, L. M., Kappeler, P. M., & Fichtel, C. (2017). Grunt to go — Vocal coordination of group movements in redfronted lemurs. *Ethology*, *123*(12), 894–905. <https://doi.org/10.1111/eth.12663>
- Stirling, I., & Thomas, J. A. (2003). Relationships between underwater vocalizations and mating systems in phocid seals. *Aquatic Mammals*, *29*(2), 227–246.
- Swedell, L., & Plummer, T. (2012). A Papionin Multilevel Society as a Model for Hominin Social Evolution. *International Journal of Primatology*, *33*(5), 1165–1193. <https://doi.org/10.1007/s10764-012-9600-9>
- Takahashi, D. Y., Narayanan, D. Z., & Ghazanfar, A. A. (2013). Coupled oscillator dynamics of vocal turn-taking in monkeys. *Current Biology*, *23*(21), 2162–2168. <https://doi.org/10.1016/j.cub.2013.09.005>
- Teichroeb, J. A., Wikberg, E. C., & Sicotte, P. (2009). Female dispersal patterns in six groups of ursine colobus (*Colobus vellerosus*): Infanticide avoidance is important. *Behaviour*, *146*(4–5), 551–582. <https://doi.org/10.1163/156853909X426363>

- Thierry, B. (2007). Unity in diversity: Lessons from macaque societies. *Evolutionary Anthropology: Issues, News, and Reviews*, 16(6), 224–238. <https://doi.org/10.1002/evan.20147>
- Tibbetts, E. A., & Dale, J. (2007). Individual recognition: it is good to be different. *Trends in Ecology and Evolution*, 22(10), 529–537. <https://doi.org/10.1016/j.tree.2007.09.001>
- Tiddi, B., di Sorrentino, E. P., Fischer, J., & Schino, G. (2017). Acquisition and functional consequences of social knowledge in macaques. *Royal Society Open Science*, 4(2), 160639. <https://doi.org/10.1098/rsos.160639>
- Tilson, Ronald, L., & Hamilton, W. J. (1984). Social dominance and feeding patterns of spotted hyaenas. *Animal Behaviour*, 32, 715–724. [https://doi.org/10.1016/S0003-3472\(84\)80147-5](https://doi.org/10.1016/S0003-3472(84)80147-5)
- Toarmino, C. R., Wong, L., & Miller, C. T. (2017). Audience affects decision-making in a marmoset communication network. *Biology Letters*, 13(1), 3–6. <https://doi.org/10.1098/rsbl.2016.0934>
- Tomasello, M., & Call, J. (1997). *Primate cognition*. New York: Oxford University Press.
- Townsend, S. W., Deschner, T., & Zuberbühler, K. (2008). Female chimpanzees use copulation calls flexibly to prevent social competition. *PLoS ONE*, 3(6), 1–7. <https://doi.org/10.1371/journal.pone.0002431>
- van Hooff, J. A. R. A. M. (1967). The facial displays of the catarrhine monkeys and apes. In D. Morris (Ed.), *Primate ethology* (pp. 7–68). Chicago: Aldine.
- Vasconcelos, M. (2008). Transitive inference in non-human animals: An empirical and theoretical analysis. *Behavioural Processes*, 78(3), 313–334. <https://doi.org/10.1016/j.beproc.2008.02.017>
- Vokey, J. R., Rendall, D., Tangen, J. M., Parr, L. A., & de Waal, F. B. M. (2004). Visual kin recognition and family resemblance in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 118(2), 194–199. <https://doi.org/10.1037/0735-7036.118.2.194>
- Walton, B., & Kershenbaum, A. (2018). Heterospecific recognition of referential alarm calls in two species of lemur. *Bioacoustics*, 1–12. <https://doi.org/10.1080/09524622.2018.1509375>
- Watson, S. K., Townsend, S. W., Schel, A. M., Wilke, C., Wallace, E. K., Cheng, L., ... Slocombe, K. E. (2015). Vocal learning in the functionally referential food grunts of chimpanzees. *Current Biology*, 25(4), 495–499. <https://doi.org/10.1016/J.CUB.2014.12.032>
- Watts, D. P. (2000). Mountain gorilla habitat use strategies and group movements. In *On the move*.

- How and why animals travel in groups* (Vol. 60, pp. 351–374). New York: University of Chicago Press. <https://doi.org/10.1006/anbe.2000.1497>
- Weingrill, T. (2000). Infanticide and the value of male-female relationships in mountain chacma baboons. *Behaviour*, *137*, 337–359. <https://doi.org/10.1136/jme.5.3.150>
- Weingrill, T., Lycett, J. E., & Henzi, S. P. (2000). Consortship and Mating Success in Chacma Baboons (*Papio cynocephalus ursinus*). *Ethology*, *106*, 1033–1044. <https://doi.org/10.1046/j.1439-0310.2000.00616.x>
- Wheeler, B. C. (2009). Monkeys crying wolf? Tufted capuchin monkeys use anti-predator calls to usurp resources from conspecifics. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1669), 3013–3018. <https://doi.org/10.1098/rspb.2009.0544>
- Whiten, A., & Byrne, R. W. (1988). Tactical deception in primates. *Behavioral and Brain Sciences*, *11*(2), 233–244. <https://doi.org/10.1017/S0140525X00049682>
- Wich, S. A., & de Vries, H. (2006). Male monkeys remember which group members have given alarm calls. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1587), 735–740. <https://doi.org/10.1098/rspb.2005.3320>
- Wiley, R. H. (2013). Specificity and multiplicity in the recognition of individuals: implications for the evolution of social behaviour. *Biological Reviews*, *88*(1), 179–195. <https://doi.org/10.1111/j.1469-185X.2012.00246.x>
- Wilson, E. O. (1979). *Sociobiology: The New Synthesis*. Cambridge, Massachusetts: Harvard University Press.
- Wiper, S. M., & Semple, S. (2007). The Function of Teeth Chattering in Male Barbary Macaques (*Macaca sylvanus*). *American Journal of Primatology*, *69*, 1–10. <https://doi.org/10.1002/ajp>
- Wittig, R. M., Crockford, C., Langergraber, K. E., & Zuberbühler, K. (2014). Triadic social interactions operate across time: A field experiment with wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, *281*, 20133155.
- Wittig, R. M., Crockford, C., Wikberg, E., Seyfarth, R. M., & Cheney, D. L. (2007). Kin-mediated reconciliation substitutes for direct reconciliation in female baboons. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1613), 1109–1115. <https://doi.org/10.1098/rspb.2006.0203>
- Zinner, D., Arnold, M. L., & Roos, C. (2011). The strange blood: Natural hybridization in

REFERENCES

- primates. *Evolutionary Anthropology*, 20(3), 96–103. <https://doi.org/10.1002/evan.20301>
- Zuberbühler, K. (2008). Audience effects. *Current Biology*, 18(5), 1–2.
<https://doi.org/10.1016/j.cub.2007.12.041>
- Zuberbühler, K., Jenny, D., & Bshary, R. (1999). The predator deterrence function of primate alarm calls. *Ethology*, 105(6), 477–490.

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DECLARATION

I hereby declare that I have written this dissertation independently and with no other aids or sources than quoted.

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Lauriane Faraut

