Climatic, social, and reproductive influences on behavioural thermoregulation in a female-dominated lemur

Timothy M. Eppley [a,b,*], Julia Watzek [c], Katie Hall [d], Giuseppe Donati [b]

[a] Biozentrum Grindel, Department of Animal Ecology and Conservation, University of Hamburg, Martin-Luther-King Platz 3, Hamburg 20146, Germany

[b] Nocturnal Primate Research Group, Department of Social Sciences, Oxford Brookes University, Gipsy Lane, Oxford, OX3 0BP, United Kingdom

[c] Department of Psychology, Language Research Center, Georgia State University, PO Box 5010, Atlanta, GA 30302, United States of America

[d] Chicago Zoological Society – Brookfield Zoo, 3300 Golf Road, Brookfield, IL 60513, United States of America

[*]Correspondence:

Timothy M. Eppley
Biozentrum Grindel
Department of Animal Ecology and Conservation
University of Hamburg
Martin-Luther-King Platz 3
Hamburg 20146, Germany
E-mail: eppleyti@gmail.com

Abstract

It is well-established that social rank in a large group confers a higher adaptive value to a dominant individual relative to others, though there is scant evidence that members of small social groups either have similar social standing or maintain strict dominance. We aimed to determine whether members of small social groups, using the southern bamboo lemur (*Hapalemur meridionalis*) as a model, gain rank-related benefits. We first established a dominance hierarchy through a network-based analysis of win-loss interactions, which showed that adult females maintained social dominance within their groups, similar to many strepsirrhine species. To address whether dominant individuals gained rank-related benefits, we then explored how social dynamics may permit access to resting huddles, which provide a physiological benefit. Social thermoregulation, i.e. huddling, is a behavioural energy conservation mechanism, and among many mammals is a direct response to decreasing ambient temperatures. As such, huddling behaviour may have evolved among social animals because of its potential direct and indirect benefits. To examine the effect of dominance rank within small social groups on huddling inclusion, we used generalized linear mixed-effects models to predict the likelihood of huddling to occur during resting bouts from climatic (e.g., temperature, precipitation), social (e.g., affiliation, dominance rank, grooming) and reproductive (e.g., access, infant protection) variables. We found that colder temperatures, especially during shorter resting bouts, increased the likelihood of huddling. Grooming between partners with a high discrepancy in rank increased huddling. Additionally, huddling increased during the reproductive season, potentially offering greater opportunity for males to gain favour with sexually receptive females, and also when new-borns were present, providing essential thermal maintenance and potential anti-predator protection to infants. Taken as a whole, our results suggest that even in small social groups, females gain rank-related benefits by controlling access to huddles, i.e., the intrinsic benefits of social thermoregulation.

Keywords: female dominance; grooming; *Hapalemur meridionalis*; huddling; Madagascar; Primates; sociality; southern bamboo lemur

Introduction

Social thermoregulation is a behavioural energy conservation mechanism (Canals et al., 1989; Kauffman et al., 2003; Madison, 1984; Scantlebury et al., 2006; West & Dublin, 1984), achieved via hunched and/or curled positions in physical contact with conspecifics (Gilbert et al., 2010; Hayes 2000). Observed in numerous avian and mammalian taxa, this is often referred to as huddling (Gilbert et al., 2010; Terrien et al., 2011). Huddling confers higher and more constant body temperatures than solitary resting (Gilbert et al., 2010; McFarland et al., 2015; Nuñez-Villegas et al., 2014) and is a typical behavioural response to thermal stress (Canals & Bozinovic, 2011; Ebensperger, 2001; Gilbert et al., 2008; Sugita & Ueda, 2013). In fact, behavioural thermoregulation by small mammals can prevent death under extremely low temperatures (Ivanov, 2006); thus, huddling behaviour may have evolved among social animals because of its potential fitness benefits (Gilbert et al., 2007; McFarland & Majolo, 2013; Nuñez-Villegas et al., 2014).

It is widely accepted that socially dominant individuals enjoy rank-related benefits (Clutton-Brock, 1988; Pusey & Packer, 1997; Silk, 2007; Smith et al., 2007; Stockley & Bro-

Jørgensen, 2011). These benefits may include privileged access to resources such as food (Isbell et al., 1999), mating partners (Alberts et al., 2006), increased anti-predator behaviour (Hegner, 1985), reduced severity of injury in agonistic conflicts (Pusey & Packer, 1997), ectoparasite removal (Akinyi et al., 2013; Mooring et al. 2004), and potentially overall better health, though stress may be elevated (Gesquiere et al., 2011; Sapolsky, 2005). Ultimately, benefits from social dominance lead to greater reproductive success (Cowlishaw & Dunbar, 1991; Ellis, 1995; Ostner et al., 2008; Pusey et al., 1997; Rodriguez-Llanes et al., 2009; Surbeck et al., 2011).

Social connections have a direct influence on thermoregulation, whereby individuals in large social groups that maintain a greater number of affiliative relationships will experience improved thermoregulation (McFarland et al., 2015). In fact, it has been shown that the more social partners a Barbary macaque (*Macaca sylvanus*) or a vervet monkey (*Chlorocebus pygerythrus*) has, the more likely the individual will be to survive an extremely cold winter, compared to individuals with fewer social partners (McFarland & Majolo, 2013; McFarland et al. 2015). Bonin flying foxes (*Pteropus pselaphon*) increase huddling as a response to cold temperatures, a behaviour that is exploited by males as female-defence polygyny, thus using huddles to defend their potential future mating opportunities (Sugita & Ueda, 2013). This slightly contrasts with what has been observed in Siberian flying squirrels (*Pteromys volans*), where huddling was driven by subsequent mating, yet not in addition to cold ambient temperatures (Selonen et al. 2014). In vervet monkeys, males with more female social partners maintained higher minimum and mean body temperatures, but those with more male social partners had higher fluctuations in temperature, likely due to intrasexual competition during the mating season (Henzi et al., 2017). These examples demonstrate how population social systems, and an individual's social network, can influence thermoregulatory capabilities in large social groups; however, how individuals from a small social group navigate huddling is less understood.

In primates, rank-related benefit hypotheses have mostly been tested in large and gregarious social species (Majolo et al., 2012; Silk, 2007), e.g., tufted capuchins (*Cebus apella nigritus*; Tiddi et al., 2012), baboons (*Papio* spp.; Altmann & Alberts, 2003), macaques (*Macaca* spp.; Rodriguez-Llanes et al., 2009; *Macaca assamensis*; Ostner et al., 2008), and chimpanzees (*Pan troglodytes* ssp.; Pusey et al., 1997). Studies of strepsirrhine social dynamics have also focused on the most gregarious species (*Eulemur* spp. *Lemur catta*, and *Propithecus verreauxi*) (van Schaik & Kappeler, 1993; Norscia et al., 2009; Port et al. 2009). Bamboo lemurs (*Hapalemur* spp.) live in small and/or family-unit sized groups (Eppley et al. 2016d; Grassi 2006; Nievergelt et al., 2002; Tan, 1999); within the *Lemuridae* family, they present an atypical study system. Whereas social rank in a large group confers a higher adaptive value to a dominant individual relative to others (Silk, 2007), there is scant evidence that members of small, family-unit social groups either have similar social standing or maintain strict dominance. The rank-related costs and benefits of living in pair-bonded and/or small social groups are often overlooked, making smaller social groups an interesting model to test whether higher dominance rank truly confers intrinsic benefits, and how this varies by sex.

Additionally, many lemur genera are known to exhibit female dominance within their social groups (Richard, 1987; van Schaik & Kappeler, 1993, 1996; Wright, 1999). Studies of lemur social dominance have typically focused on targeted aggression, travel initiation, feeding priority, and directional grooming (Jolly, 1966, 1984; Kappeler, 1990; Norscia & Palagi, 2015; Overdorff et al., 2005; Waeber & Hemelrijk, 2003). In this study, we aimed to establish the social structure of a lemur species living in small social groups, the southern bamboo lemur

(*Hapalemur meridionalis*), by examining these variables. We first extracted an aggression network based on win-loss interactions to determine individual dominance ranks within each social group. As *H. meridionalis* is a close congener to *H. alaotrensis*, we predicted that southern bamboo lemur groups will also exhibit female dominance. Furthermore, we aimed to determine whether members of a small social group maintain strict dominance and gain rank-related benefits by exploring how social dynamics may permit access to resting huddles, which provide a physiological benefit.

Malagasy strepsirrhines employ a variety of thermoregulatory strategies to cope with cold, resource-deficient months, including huddling (Donati et al. 2011; Ostner 2002). A recent study showed that huddling by southern bamboo lemurs conferred an immediate thermoregulatory effect, which assisted in the maintenance of optimal body temperature during resting bouts (Eppley et al., 2017). In our observations, it was often the case that adult females huddled together or with juveniles before allowing adult males to join. As such, we questioned which factors affected an individual's inclusion in a social thermoregulation huddle. We predicted that dominant individuals (i.e., females) will influence others' access to/inclusion in resting huddles.

Most lemurs are sexually quiescent throughout much of the year and exhibit strict seasonal breeding (Brockman and van Schaik, 2005; Jolly, 1967; Rasmussen, 1985; Sauther 1998; for exceptions see: Tecot, 2010), including *H. meridionalis* (Eppley et al., 2016b). In terms of group sociality, this led us to consider that adult females would adjust their relationships during breeding times in order to benefit from their dominance ranking. Grooming may be a way for potential mates to assess one another, thus we predicted that adult female *H. meridionalis* would utilize their dominant social position to engage in more grooming within a resting bout, before or after a huddle, near or during the mating season (June/July) when females become sexually receptive (Barelli et al., 2011; Colmenares et al., 2002; Gumert 2007; Hemelrijk et al., 1992; Norscia et al., 2009). An increase in grooming during this time would indicate that in addition to intrinsic benefits, grooming has a long-term reproductive benefit.

Conversely, once offspring have been born (November/December), female priorities may shift away from mate assessment (via grooming) towards protecting infants from thermoregulatory stress and predators (via huddling); that is, the social function of grooming may be less important to new mothers than the protective function of huddling. Thus, we predicted less grooming as a precursor to huddling when a new-born infant was present, so that the dual benefits of behavioural thermoregulation and anti-predator protection could be more quickly provided to the mother and infant.

Methods

Ethical note

Data were collected in accordance with the ASAB/ABS Guidelines for Use of Animals in Research. This study was carried out under the Accord de Collaboration among the University of Antananarivo and the University of Hamburg. Research protocols were approved and permits authorized by Commission Tripartite of the Direction des Eaux et Forêts de Madagascar (Research Authorization N° 240/12/MEF/SG/DGF/DCB.SAP/SCB du 17/09/2012), adhering to the legal requirements of Madagascar.

Study Site and Species

We conducted our study in the Mandena Conservation Zone (24°95'S 46°99'E), a 230-hectare degraded littoral forest fragment and swamp located along the southeast coast of Madagascar (Eppley et al., 2015a). Our study species was the southern bamboo lemur (*Hapalemur meridionalis*), a medium-sized strepsirrhine (ca. 1.1 kg) characterized by a folivorous diet (Eppley et al., 2011, 2015b, 2016a). This species maintains small social groups, with an average of 5.6 individuals, typically consisting of one to two adult male(s) and one to two breeding adult female(s) that are in constant daily contact (Table 1; Eppley et al., 2015a). Additionally, one of the bamboo lemur social groups in Mandena (Group 4) maintains a close long-term affiliation with an adult female ring-tailed lemur (*Lemur catta*). This *L. catta* has been regularly observed with this group since 2008, and throughout the course of our study she played an integral role in the social dynamics of this group (Eppley et al., 2015c).

Southern bamboo lemurs exhibit seasonal reproduction, similar to most lemuriformes (Wright, 1999). Bamboo lemur species have been recorded to mate between June and July, providing a gestation length of approximately 130-140 days (Tan, 2006; Wright, 1990). In spite of not observing *H. meridionalis* copulation during the study period, we relied on published congener observations to approximate their gestation length; infants were first observed in mid-November (Eppley et al., 2016b). Therefore, we considered the months of June and July to be the "mating season", during which time the females are likely to be sexually receptive. Though we did not conduct any genetic analyses to determine the relationships between individuals, it should be noted that there was only one adult male per group studied. As *H. meridionalis* groups in Mandena display territoriality and minimal home range overlap (Eppley et al., 2015a, 2016d), we presume it unlikely any extra-pair copulations occurred and each group's resident male fathered the infant(s) within that group (Eppley et al. 2016b).

Behavioural data

All adult individuals were fitted with collars, including colour-coded pendants that allowed for individual identification (Eppley et al., 2015b). From January to December 2013, focal observations were conducted on adult individuals within three social groups, with data collected during both full- and half-day focal follows, accounting for 1,762 h (N = 195 days).

We recorded instantaneously every 5 min during resting bouts when the focal was in physical contact (i.e. huddling) with a group member, recording all individuals in the huddle (Eppley et al., 2017). This permitted the proportion of huddling from the total resting bout time to be calculated. To establish social affiliation (i.e., proximity) of *H. meridionalis*, we recorded the nearest neighbour to the focal via instantaneous sampling every 5 min, categorized as close (≤ 3 m) and far (> 3 m). Additionally, continuous sampling (to the second) was conducted for all grooming occurrences, noting the initiator, recipient, and whether the interaction was unidirectional (i.e., one-way) or mutual (i.e., the action was reciprocated by the recipient during the bout). These data allowed us to calculate daily proximity proportions of the focal individual towards all other individuals within the group. To determine a dominance hierarchy, we recorded *ad libitum* all observed agonistic behaviours (e.g., vocal threat, open mouth display, chase, hit/fight, and wound), while also recording the initiator, recipient, and any submissive behaviours, e.g., whimper, avoid/reposition, or flee (Waeber & Hemelrijk, 2003). Depending on the outcome, we were able to assign the encounter as a win, loss, or draw for the focal individual. It should be noted that although our focal was always an adult or subadult, juveniles (and the *L. catta* in the case of Group 4) were included as nearest neighbours and as initiators/recipients of grooming bouts and agonistic interactions. Furthermore, travel initiation is often used as a measure of social dominance (Schaller, 1963; Tecot & Romine, 2012; but see Leca et al., 2003), thus we recorded all occurrences when the focal individual initiated travel from a feeding or resting location, in which more than half of the group followed within 60 seconds (Waeber & Hemelrijk, 2003).

Data analyses

A total of $N = 428$ dyadic win-loss interactions were used to construct aggression networks with the *network* package (Butts et al., 2015) and to extract rank information using the *Perc* package (Fujii et al., 2015) in R statistical software (R Core Team, 2016). Note that 28 draws were excluded from analyses. We used the percolation and conductance approach to extract dominance ranks by combining information from direct dominance interactions with information from indirect interactions across the social network (Fushing et al., 2011a, 2011b). We transformed the ordinal dominance ranks into the proportion of group members that an individual outranks (i.e., 0 for the lowest rank, 1 for the highest) to standardize rank information across the different group sizes. We used Fisher's exact test to determine whether males and females who initiate fights differed in their likelihood to target males or females. Additionally, we used a two-tailed *t*-test to assess whether travel initiation rates differed for males and females.

To determine which factors influenced the occurrence of huddling behaviour between two lemurs during rest bouts, we fitted generalized linear mixed-effects models (GLMMs) with huddling as a binomial dependent variable. As fixed effects, both as independent terms and in interactions, we included the sex and rank of the focal, the partner's sex and rank, their affiliative tendency, and their rank differential (with positive numbers indicating that the partner was higher-ranking than the focal and negative numbers indicating that the partner was lower-ranking than the focal). We also included as fixed effects whether the focal groomed the partner within 60 minutes before a resting bout (0/1) or within 60 minutes after a rest bout (0/1), as well as the duration (min) of each bout. While we recorded grooming directionality and grooming duration to the second, grooming given and grooming received were strongly correlated (pre-huddle: $r_{2016} = 0.97$, post-huddle: $r_{2016} = 0.95$) and grooming duration was heavily zero-inflated (85% of values were zeros). Due to this, we have a binary variable and only considered grooming given. In addition, for the months June and July (i.e., approximate period of sexually receptivity), we included whether the focal and/or partner was a future offspring-bearing female (0/1), and for the months of November and December, we recorded when an infant was present (0/1) during resting bouts. Finally, we included climatic variables as fixed effects, specifically temperature (°C), as the mean ambient temperature from the nearest data-logger during the rest bout, daily total precipitation (mm), and the general season (dry or wet). We standardized duration, ambient temperature, and precipitation because they were on very different scales of magnitude. As random effects, we included individual identity of the focal lemur and their (potential) partner to account for different baseline rates of huddling.

We used an information-theoretic approach with model averaging to generate a set of candidate models and assess the relative strength of evidence for our hypotheses (Burnham & Anderson, 2002). We inspected the Variance Inflation Factors (VIF) of a full model, including all fixed effects, to assess multicollinearity. To obtain unbiased parameter estimates, we did not include collinear terms (VIF > 3) in the same model. Highly related predictors could, however, occur in separate models of the model set. We ranked the models using Akaike's Information Criterion corrected for finite sample sizes (AICc) and defined a subset of top models as those models within two AICc units from the best model ($\Delta_i < 2$). We then computed the model-averaged parameter estimates and the relative importance for each term included in this model set. Importance is the sum of the Akaike weights w_i of all models which include the term in question. As model weights represent the probability of a model to be the best model in the model set and thus reflect model uncertainty, importance can be understood as the likelihood of a term to be included in the best model. We used the *lme4* (Bates et al., 2015) and *MuMIn* (Bartoń, 2016) packages in R statistical software (R Core Team, 2016) for these analyses.

Results

Social organization

Female *H. meridionalis* displayed social dominance over males in Mandena. In 94.4% of all dyadic win-loss interactions, the initiator won the fight. Females initiated 92.5% of fights and were twice as likely to target a male (rather than a female) than were males who initiated fights, (Fisher's exact test: odds ratio = 0.46, 95% CI [0.21, 1.04], $p = 0.04$). Figure 1 shows the aggression network extracted from these interactions. Females occupied the highest dominance ranks in each of the three groups and had higher average ranks than males (rank proportion female: mean ± SD = 0.69 ± 0.33, male: mean ± SD = 0.26 ± 0.25, $t(14.00) = 3.00$, $p = 0.01$). Considering context, 79.8% of all observed agonism was over access to food, with 99.7% of these interactions won by females. In terms of non-agonistic dominance, females initiated travel at significantly higher rates per hour than males (female: mean ± SD = 0.26 ± 0.14, male: mean ± SD = 0.10 ± 0.06, $t(8.57) = 2.59$, $p = 0.03$). Despite social dominance strongly skewed in favour of females, affiliation (via proximity) did not vary by dyad type, i.e., female-female, male-female, male-male (ANOVA: $F_{2, 68} = 0.01$, $p = 0.99$).

Huddling Behaviour

The two top models to explain the occurrence of huddling between two lemurs both included as significant terms: temperature, duration, and their interaction; pre- and post-bout grooming, and their interaction; interaction of rank differential with pre-bout grooming; whether an infant was present; and whether a female would bear offspring later in the season (Table 2). Model 2 additionally included a significant interaction of rest bout duration with pre-bout grooming. The two models were similarly well supported by the data, with Model 1 being 1.3 times more likely to be the best model (evidence ratio $w_1/w_2 = 0.56/0.44$).

Southern bamboo lemurs were 10 times more likely not to huddle than to huddle during a resting bout (odds ratio $^{1}/_{0.09}$). When ambient temperatures dropped by one standard deviation (5.02°C), however, lemurs were 1.6 to 2.4 times more likely to huddle. This effect of temperature on huddling was stronger when rest bouts were short: a decrease in resting duration by one standard deviation (45.87 min) further increased the odds of huddling by 1.2 to 1.7 (Figure 2; temperature*duration interaction). Additionally, females that would bear offspring later in the year (November/December) were 1.5 to 4.0 times more likely to huddle during the period of sexual receptivity (June/July). Furthermore, focal individuals increased their odds of huddling by a factor of 5.3 when an infant was present. Finally, lemurs were about three to four times more likely to huddle if the focal groomed the partner before the rest bout (odds ratio = 3.78), after the rest bout (odds ratio = 2.66), or both (pre- and post-bout interaction, odds ratios 3.78*2.66*0.41 = 4.12).

Pre-bout grooming was moderated by the relative ranks of the focal and partner to each other. Grooming before the rest bout increased the focal's chances to huddle by an additional factor of 1.4 for every hierarchy-level that the partner outranked the focal (Figure 3; pre-bout grooming*rank differential interaction). That is, pre-bout grooming was most effective in leading to huddling when it occurred with the most dominant partners (highest rank differential). Model 2 further suggests that pre-bout grooming was more likely to increase odds of huddling when rest bouts were short (duration*pre-bout grooming interaction); however, the strength of the evidence is weaker for this interaction (relative importance: 0.44).

Discussion

In this study, we aimed to address four main hypotheses. We sought to determine the social organization of *H. meridionalis* and found that female bamboo lemurs outrank males. Following this, we questioned whether one's position in the social hierarchy affected an individual's inclusion in a social thermoregulation huddle, and found that an individual's access to a huddle was influenced by pre- and post-huddle grooming bouts with higher ranking female partners. Huddling provides a thermoregulatory mechanism (Eppley et al., 2017), and the temperature*duration interaction showed that huddling was most frequent when ambient temperatures were low and the resting bout was of short duration. Though neither the sex nor rank of the focal or the partner were included in the top models to predict huddling, this is because it is captured in the rank differential. Interestingly, affiliative tendency was not included in either of the best-fit models, thus proximity cannot explain dyadic huddling choices. High-ranking females huddled when focal subjects groomed with them beforehand; thus, both partners accrued benefits from grooming and huddling. In contrast, when high-ranking individuals groomed, their likelihood to huddle did not increase. These results highlight that the benefits of social living are not equally enjoyed by all members of small social groups; female *H. meridionalis* exert social dominance over males to control access to huddles, although further investigation into the costs and benefits of other social behaviours are warranted. Additionally, we tested two predictions related to female reproductive strategies: mate assessment and infant protection. Sexually receptive females, and later those with infants, increased their rates of huddling relative to others. This behavioural adjustment provided not only thermoregulatory benefits to huddling partners and offspring, but also protection of the infant from potential predators. Females and their offspring therefore gained rank-related benefits from allowing lower-ranked males to participate in thermoregulatory huddles.

Social organization: are females dominant?

Bamboo lemurs are reported to have a flexible social organization, with the Lac Alaotran gentle lemur (*H. alaotrensis*), the golden bamboo lemur (*H. aureus*), the gray bamboo lemur (*H. griseus*), and the western lesser bamboo lemur (*H. occidentalis*) all recorded to live in monogamous pairs, polygynous groups, and occasionally multi-male / multi-female social groups (Goodman & Schütz, 2000; Grassi, 2006; Mutschler et al., 2000; Nievergelt et al., 2002; Tan, 1999, 2006). Considering the genera as a whole, the *H. meridionalis* population in Mandena is analogous, with both monogamous and polygamous social groups coexisting. Interestingly, the polygamous social group, i.e. two breeding adult females, was the group with the female *L. catta*. The ring-tailed lemur within group 4 was shown to be dominant over her *H. meridionalis* group-mates. It is plausible that her large-bodied presence provided increased anti-predator vigilance and territorial resource defence (Eppley et al., 2015c), thus potentially decreasing the amount of time these bamboo lemurs needed to defend their resources.

Though less common, some mammals display female social dominance, e.g., hyrax (*Procavia capensis*; Koren et al., 2006), giant otter (*Pteronura brasiliensis*; Duplaix, 1980), and spotted hyaena (*Crocuta crocuta*; Smale et al., 1993). Similarly, female *H. meridionalis* maintained social dominance over conspecific males, outranking adult males in each group. This is similar to what was previously recorded among congeners *H. alaotrensis* (Waeber & Hemelrijk, 2003) and *H. griseus* (Digby & Stevens, 2007), among many other lemur genera e.g., *Lemur* (Jolly, 1966, 1984; Kappeler, 1990; Sauther et al., 1999), *Eulemur* (Digby & Stevens, 2007), *Indri* (Pollock, 1979; Powzyk, 1997), *Propithecus* (Powzyk, 1997), *Avahi* (Ramanankirahina et al., 2011), *Microcebus* (Radespiel & Zimmerman, 2001), and *Varecia* (Overdorff et al., 2005); although some brown lemurs (*Eulemur* spp.) and sifaka (*Propithecus* spp.) have an egalitarian social structure (Pereira et al., 1990; Pereira & Kappeler, 1997; Sterck et al., 1997). This included the maintenance of female feeding priority over potentially limited resources such as ripe fruit, but also typical social dominance in which agonistic behaviours occurred under non-feeding contexts. Furthermore, females initiated group travel direction more often than males. Taken as a whole, these social behaviours strongly support females as maintaining dominance within their respective groups. Coupled with female feeding and social dominance, female *H. meridionalis* did not maintain stronger affiliations among themselves, and males were not peripheral within the social group. This contrasts with a study of a close congener, *H. griseus*, which showed that males were socially peripheral (Grassi, 2002).

Do dominant females control access to thermoregulatory huddles via grooming?

Social affiliation has been shown to influence huddling partners in gregarious primate species, e.g., vervet monkeys (*Chlorocebus pygerythrus*; McFarland et al., 2015), Barbary macaque (*Macaca sylvanus*; McFarland & Majolo, 2013), Japanese macaques (*Macaca fuscata*; Takahashi, 1997), and Tibetan macaques (*Macaca thibetana*; Ogawa & Takahashi, 2003);

however, proximity affiliation was not included in the top models predicting huddling behaviour by southern bamboo lemurs. On a finer scale of affiliation, both pre- and post- resting bout grooming were significant predictors of whether huddling occurred. Considering group-level context, it is important to remember that these results are based on dyadic interactions. Our subjective impression of many of the resting bouts were that adult female(s) were already huddling together and/or with juveniles before allowing males to join; however, due to the nature of our focal data collection, we are unable to determine how many/which individuals were in the huddle longitudinally before our focal joined.

Unlike some primates which exhibit minimal amounts of mutual grooming, e.g. Verreaux's sifaka (*Propithecus verreauxi*; Lewis, 2010), greater than 70% of all *H. meridionalis* grooming bouts within one hour before or after a resting bout were bidirectional. This is possibly due to bamboo lemur groups being small rather than larger, more gregarious lemur species' groups. Thus, grooming reciprocity may be necessary to maintain cooperation within their smaller groups. Bamboo lemurs regularly display allomaternal care, with males and other group members often carrying infants to assist the mother (Eppley et al. 2015c; TM Eppley, unpublished data; Wright 1990), and so reciprocating grooming exchanges and joining thermoregulatory huddles between sexes may ensure continued cooperation among group members and provide protection for infants.

Additionally, a function of grooming is to increase the loft of the fur to increase thermal insulation (McFarland et al., 2016); therefore, mutual grooming within the hour preceding or following huddling serves both a functional and a social purpose beneficial to both partners. Thus, grooming appeared to be integral for the occurrence of huddling during a resting bout. However, the rate of huddling subsequently increased if the pre-resting bout grooming was with an individual of greater dominance rank (Fig. 3). The *L. catta* was also involved in grooming bouts before and after huddles. It is possible that due to the larger body size of the *L. catta*, she provided greater surface area with which group-mates could huddle (Fig. 4). While there have been numerous observations of interspecies grooming (Heymann and Buchanan-Smith, 2000), the unusual social dynamic we observed is the only example, to our knowledge, of longitudinally maintained interspecies reciprocity in the wild.

Do females huddle more during the mating season?

Sexually receptive females huddled significantly more in general during their typical breeding season (June-July), potentially allowing for reciprocal mate assessment. While the breeding season occurs during the coldest months, which may be viewed as a caveat, it is important to note that both temperature and duration were controlled for within the analyses. Thus, it may be that increased behavioural thermoregulation facilitated future breeding opportunities, similar to what has been recorded for Bonin flying foxes (Sugita & Ueda, 2013), Siberian flying squirrels (*Pteromys volans*; Selonen et al., 2013), and suggested for Abert's squirrels (*Sciurus aberti*; Edelman & Koprowski, 2007).

Does infant presence reduce pre-huddle grooming?

During the first two months of an infant being in the group (Nov./Dec.), huddling was shown to significantly increase for individuals that had an infant present. As allomaternal care is frequently observed among *H. meridionalis* group mates (e.g., adult males and juveniles; TM Eppley, unpublished data), including the female *L. catta* (Eppley et al., 2015c), the mother was not always present within these huddles with the infant. This was expected as even some typically asocial mammals will communally nest in order to defray the high thermoregulatory costs of endothermic heat production during cold seasons, e.g., Abert's squirrels (*Sciurus aberti*; Edelman & Koprowski, 2007), red squirrels (*Tamiasciurus hudsonicus*; Williams et al., 2013), southern flying squirrels (*Glaucomys volans*; Stapp et al., 1991; Merritt et al. 2001), and eastern pygmy-possums (*Cercartetus nanus*; Namekata & Geiser, 2009). The potential benefits of this include not only greater thermoregulatory benefits for those individuals involved (Eppley et al., 2017), but may provide vital anti-predator protection for young offspring when included. This has been observed in many species, with groups forming positional protection around infants (Caro et al., 2004), e.g., African elephant (*Loxodonta africana*; Loveridge et al., 2006), American bison (*Bison bison*; Carbyn & Trottier, 1987), and elk (*Cervus elaphus*; Gower et al., 2008). Though huddling in the presence of infants increased, our prediction that there would be a lower threshold of duration of grooming prior to huddling was not supported: similar to before infants were born, grooming (especially with a higher-ranking individual, i.e., adult female) increased chances of accessing a resting huddle, but there was no interaction of infant presence with pre- or post-bout grooming.

While it is possible that these huddles may provide an additional anti-predator role, southern bamboo lemurs have been observed to both feed and sleep on the ground which suggests that overall predation pressure may be reduced within this fragmented habitat (Eppley et al., 2016a, 2016c). Japanese macaques living on the island of Shodoshima also experience a lack of predation, yet have been observed to form clusters of greater than 100 individuals, though their highly tolerant social organization has been causally suggested (Zhang & Watanabe, 2007). In spite of this, *Hapalemur* spp. are susceptible to both aerial and terrestrial predation (Karpanty

& Wright, 2007), and while the potential risk may be reduced in Mandena, predation has still been observed (Eppley & Ravelomanantsoa, 2015).

Conclusion

Within the case of *H. meridionalis*, a species that lives in small, female-dominant social groups, grooming often led to huddling during resting bouts, especially when males groomed females. Huddles are vital as they provide a necessary physiological benefit through behavioural thermoregulation. We also showed that huddling increased when new-borns were present, providing essential thermal benefits and potential anti-predator protection to infants. These results support the hypothesis that females benefit from their higher social dominance and have greater reproductive success because of it.

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Table 1. Demography of *H. meridionalis* focal groups in Mandena.

	Individual	Sex	Body weight (g)	Age class	Months present
Group 1					
	C[*]	F	1125	Adult	Jan. – Dec.
	D	F	1150	Adult	Jan. – Mar.[†]
	E	F	975	Subadult	Jan. – Sept.[§]
	P	M	975	Adult	Jan. – Dec.
	F	F	625	Juvenile	Jan. – Dec.
Group 2					
	I[*]	F	1100	Adult	Jan. – Dec.
	H	M	1075	Adult	Jan. – Dec.
	J	M	450	Juvenile	Jan. – Dec.
Group 4					
	R[*]	F	1100	Adult	Jan. – Dec.
	S[*]	F	1075	Adult	Jan. – Dec.
	Q	M	900	Subadult	Jan. – Dec.[§]
	V	M	na	Adult	Jan. – Dec.
	U	M	na	Juvenile	Jan. – Dec.
	X	M	na	Juvenile	Jan. – Dec.
	Z	F	na	Juvenile	Jan. – Dec.
	Y - *Lemur catta*	F	na	Adult	Jan. – Dec.

* Birthed an infant between late October and early December 2013 (Eppley et al., 2016b)

na not available

[†] Individual died (Eppley & Ravelomanantsoa, 2015)

[§] Individual dispersed during last month present

Table 2. Model-averaged GLMM parameters for predicting the occurrence of huddling behaviour

Term	β	*SE*	95% CI	OR	OR 95% CI	Model	Importance
Intercept	-2.38***	0.27	(-2.91, -1.85)	0.09	(0.05, 0.16)	1, 2	1
Temperature[a]	-0.66***	0.10	(-0.86, -0.47)	0.52	(0.42, 0.63)	1, 2	1
Duration[a]	0.61***	0.10	(0.41, 0.81)	1.84	(1.50, 2.26)	1, 2	1
Temperature * Duration	-0.35***	0.09	(-0.52, -0.18)	0.70	(0.59, 0.84)	1, 2	1
Future Mother (Jun/Jul)	0.88***	0.26	(0.37, 1.39)	2.42	(1.45, 4.02)	1, 2	1
Infant Present (Nov/Dec)	1.67***	0.44	(0.82, 2.53)	5.32	(2.26, 12.53)	1, 2	1
Pre-bout Grooming (Pre)	1.33***	0.29	(0.77, 1.89)	3.78	(2.15, 6.65)	1, 2	1
Post-bout Grooming (Post)	0.98***	0.25	(0.49, 1.46)	2.66	(1.64, 4.31)	1, 2	1
Pre * Post	-0.89	0.52	(-1.91, 0.13)	0.41	(0.15, 1.14)	1, 2	1
Rank Differential	-0.03	0.05	(-0.14, 0.08)	0.97	(0.87, 1.08)	1, 2	1
Pre * Rank Differential	0.34**	0.11	(0.12, 0.55)	1.40	(1.13, 1.74)	1, 2	1
Post * Rank Differential	0.09	0.09	(-0.08, 0.26)	1.09	(0.92, 1.30)	1, 2	1
Duration * Pre	-0.47*	0.27	(-0.88, -0.06)	0.62	(0.41, 0.94)	2	0.44
Duration * Post	-0.15	0.15	(-0.52, 0.22)	0.86	(0.59, 1.25)	2	0.44
Duration * Rank Differential	0.03	0.03	(-0.03, 0.10)	1.03	(0.97, 1.10)	2	0.44

Note. N = 1351. Akaike weights: $w_1 = 0.56$, $w_2 = 0.44$. Difference in AICc values between Model *i* and the model with the lowest AICc, Model 1: $\Delta_1 = 0.00$, $\Delta_2 = 0.46$. Parameters shown are model-averaged parameter estimates (β), unconditional standard errors which incorporate model uncertainty (*SE*), odds ratios (OR), 95% confidence intervals, models that included the term, and relative importance. [a]Standardized with the following original means ± SD. Temperature: 23.75 ± 5.02; Duration: 57.53 ± 45.87. $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

Figure Legends

Figure 1. Win-loss networks for three groups of southern bamboo lemurs (*H. meridionalis*) in Mandena. Node numbers and sizes indicate dominance rank, while the letters indicate individual IDs. 1Y indicates the *L. catta* (see text). Edge weights are proportional to the number of agonistic interactions observed for each dyad.

Figure 2. Huddle rate as a function of ambient temperature and duration (shown as a dichotomous measure for visualization purposes). Rest bouts shorter than the average of 57.53 minutes are indicated by triangles; those above by circles. Plotted lines indicate logistic linear regression models for short (dotted) and long (solid) rest bouts; shaded areas indicate 95% confidence intervals.

Figure 3. Huddle rate as a function of pre-bout grooming and rank differential. Plotted lines indicate logistic linear regression models for rest bouts with (solid) and without (dotted) prior grooming; shaded areas indicate 95% confidence intervals.

Figure 4. Three *H. meridionalis* huddling with the dominant female *L. catta* in Mandena.