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

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It is well established that social rank in a large group confers a higher adaptive value to a dominant individual relative to others, although 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 occurring 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 lower 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 when new-borns were present, providing essential thermal maintenance and potential antipredator protection to infants. Together, 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.

Social thermoregulation is a behavioural energy conservation mechanism (Canals, Rosenmann, & Bozinovic, 1989; Kauffman, Paul, Butler, & Zucker, 2003; Madison, 1984; Scantlebury, Bennett, Speakman, Pillay, & Schradin, 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, Perret, & Aujard, 2011). Huddling confers higher and more constant body temperatures than solitary resting (Gilbert et al., 2010; McFarland et al., 2015; Nuñez-Villegas, Bozinovic, & Sabat, 2014) and is a typical behavioural response to thermal stress (Canals & Bozinovic, 2011; Ebensperger, 2001; Gilbert, Robertson, Le Maho, & Ancel, 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;

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Silk, 2007; Smith, Memenis, & Holekamp, 2007; Stockley & Bro-Jørgensen, 2011). These benefits may include privileged access to resources such as food (Isbell, Pruetz, Lewis, & Young, 1999), mating partners (Alberts, Buchan, & Altmann, 2006), increased antipredator behaviour (Hegner, 1985), reduced severity of injury in agonistic conflicts (Pusey & Packer, 1997), ectoparasite removal (Akinyi et al., 2013; Mooring, Blumstein, & Stoner, 2004), and potentially overall better health, although 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, Heistermann, & Schülke, 2008; Pusey, Williams, & Goodall, 1997; Rodriguez-Llanes, Verbeke, & Finlayson, 2009; Surbeck, Mundry, & Hohmann, 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 low 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 low ambient temperatures (Selonen, Hanski, & Wistbacka, 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, probably because of 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, Lehmann, de Bortoli Vizioli, & Schino, 2012; Silk, 2007), for example tufted capuchins, *Cebus apella nigritus* (Tiddi, Aureli, & Schino, 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., ring-tailed lemur, *Lemur catta* and Verreaux's sifaka, *Propithecus verreauxi*: van Schaik & Kappeler, 1993; Norscia, Antonacci, & Palagi, 2009; Port, Clough, & Kappeler, 2009). Bamboo lemurs, *Hapalemur* spp., live in small and/or family-unit-sized groups (Eppley, Ganzhorn, & Donati, 2016d; Grassi, 2006; Nievergelt, Mutschler, Feistner, & Woodruff, 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, Erhart, & Mutschler, 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 *Hapalemur alaotrensis*, we predicted that southern bamboo lemur groups will also exhibit female dominance (Waeber & Hemelrijk, 2003). 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, Ricci, Baldi, Morelli, & Borgognini-Tarli, 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, Watzek, Dausmann, Ganzhorn, & Donati, 2017). In our observations, we often saw 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 & van Schaik, 2005; Jolly, 1967; Rasmussen, 1985; Sauther, 1998; for exceptions, see Tecot, 2010), including *H. meridionalis* (Eppley, Donati, & Ganzhorn, 2016b). In terms of group sociality, this led us to consider that adult females would adjust their relationships during breeding times to benefit from their dominance ranking. As grooming may be a way for potential mates to assess one another, 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, Reichard, & Mundry, 2011; Colmenares, Zaragoza, & Hernández-Lloreda, 2002; Gumert, 2007; Hemelrijk, van Laere & van Hooff, 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 antipredator 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