# The social and thermal competence of wild vervet monkeys

Richard McFarland[1,2], Peter Henzi[3,4], Louise Barrett[3,4]

[1] Department of Anthropology, University of Wisconsin-Madison, United States.

[2] Brain Function Research Group, School of Physiology, University of the Witwatersrand, South Africa.

[3] Department of Psychology, University of Lethbridge, Canada.

[4] Applied Behavioural Ecology and Ecosystems Research Unit, University of South Africa, South Africa.

Words: 2560 words.

As long-lived, slowly reproducing animals, primates face numerous ecological challenges to their survival and successful reproduction. The majority of primates live in groups, an adaptation widespread in the animal kingdom that can provide improved predator defense, food acquisition, and access to mating opportunities; all of which can contribute to an individual's fitness. Compared to other animal taxa, however, primates are intensely social, spending a significant amount of time forming and maintaining social relationships within their group (Dunbar 1991). There is evidence to suggest that such relationships are evolutionarily adaptive: more socially integrated individuals experience improved rates of survival and reproductive success (Silk et al. 2009; Schülke et al. 2010; McFarland & Majolo 2013; McFarland et al 2017). One argument for the adaptive value of social relationships is that they help offset the inevitable costs of group-living, which manifest in terms of increased competition for resources, such as food, safe spatial positions and mates. The patterning of social life thus represents the negotiation of individual needs within constraints imposed by others. This, in turn, is argued to have selected for a high degree of developmental plasticity and behavioral flexibility among the anthropoid primates in particular.

In addition to these social challenges, climatic variability is also known to exert strong selective pressures on ecology, behavior and physiology, and has similarly been argued to select for plasticity in the form of developmental norms of reaction, as well as individual behavioral flexibility. Most notably, it has been argued that selection for the ability to cope with and respond to rapid and extensive environmental change can explain patterns of hominin evolution, and the marked flexibility of humans compared to other animals (Potts 1998; Maslin et al. 2015). Understanding the scope and limits of primates' ability to cope with environmental variability is thus the focus of much socioecological research which, broadly speaking, attempts to answer the question of how primates solve their ecological problems with respect to the opportunities and constraints of social life. Such questions are becoming ever more pressing in the context of the imminent threat of global climate change to our planet's biodiversity (Thompson et al. 2005; Wiederholt & Post 2010). Approximately 60% of species are now threatened with extinction, with 75% of primate species experiencing a declining population (Estrada et al. 2017).

Our own research focuses on the behavioral and physiological strategies used by primates to deal with environmental variation, both via changes in resource availability and in terms of direct climatic effects. Specifically, we focus on the thermal physiology wild vervets (*Chlorocebus pygerythrus*), investigating whether social life compounds or ameliorates the demands made by the thermal environment. Vervet monkeys are ideal model organisms for a study of this type because they are obligatorily social, experience a wide temperature range in arid environments, and manifest a range of specialised behavioral thermoregulatory adaptations. To date, most studies on the thermal physiology of large mammals (which, generally speaking, means non-rodent species) have focused on species that are either solitary or show limited sociality (Fuller et al. 2016). Unlike these species, group-living primates potentially face a compromise between the strategies that promote physiological homeostasis and those that optimise the benefits of group-living. Our study is unique, therefore, in allowing us to probe the intersection of our animals' ecological and social strategies, the degree of flexibility they display, and what consequences this holds for survival and reproductive success. This, in turn, provides vital information concerning the long-term viability of vervets populations in the face of ongoing climate change.

Since 2008, we have been studying three groups of vervets on the Samara Private Game Reserve in the Nama Karoo, Eastern Cape, South Africa, combining behavioral, ecological, and body temperature data, to investigate individual differences in thermal competence, sociability and fitness-related traits. Samara is characterized as a high-altitude, semi-arid desert, with vervet presence mostly restricted to narrow strips of riparian *Acacia karroo* woodland along non-perennial streams (Pasternak et al. 2013). The region experiences hot, wet summers (November – March) and cold, dry winters (June – August), with minimum and maximum temperatures ranging between -5 and 40 ºC (McFarland et al. 2014). This region of South Africa is also prone to intermittent periods of drought (Hoffman et al 2009). Vervets have inhabited the semi-arid karoo biome of South Africa since at least the 18$^{th}$ century, and despite these extreme environmental conditions, are found at high population densities, with higher than average group sizes compared to other vervet populations in Africa (Pasternak et al. 2013). The rapidity of change in arid-zone thermal environments offers an excellent and feasible opportunity to track the targets of natural selection for thermal competence.

The majority of studies that have explored the effects of environmental variability on primates have tended to focus on the effect of climatic variables on behaviors crucial for survival (e.g., resting, foraging and social activity: Hill et al. 2003; Campos & Fedigan 2009; Korstjens et al. 2010; Majolo et al. 2013; McFarland et al. 2014). Importantly, only a few studies have directly collected body temperature measurements from free-ranging primates (Brain & Mitchell 1999; Mzilikaze et al. 2006; Dausman et al. 2004; Nowack et al. 2010; Thompson et al. 2014). Although these studies have provided important insights, they have been restricted to few study subjects, short study periods, or lacked detailed simultaneous data on the primates' behavior, feeding ecology and environment. Moreover, most of these studies used skin or subcutaneous body temperature measurements, which can be significantly affected by ambient temperature, ultimately providing less accurate accounts of the effect of climate on core body temperature. Consequently, the existing literature provides limited insight into the effects of environmental variability on animal's ability to thermoregulate efficiently. Our study of vervets is the first to use bio-logging technology to collect continuous long-term measurements of core body temperature from multiple individuals in a wild population, whilst simultaneously collecting detailed records of their behavior and ecology (McFarland et al. 2013). Bio-logging has allowed us to determine how efficiently a monkey regulates its body temperature (i.e., daily body temperature averages, amplitudes, minima and maxima) when exposed to environmental and social stressors.

Like all mammals, vervet monkeys are homeothermic, and typically maintain a body temperature ranging between 37 and 39 ºC (Lubbe et al. 2014). Homeothermy is the ability to maintain a core body temperature within a narrow range when subjected to a wide range of environmental temperatures. This is achieved through a combination of autonomic and behavioral processes. Autonomic processes, involving the activation of pathways in the anterior hypothalamus to regulate the balance of heat production and loss, can be costly in terms of energy expenditure at low temperatures, and water loss (i.e., evaporative sweat) at high temperatures. To help alleviate these costs, animals can also engage in behaviors that help to keep their body warm or cold, such as changing posture or selecting appropriate microclimates. Vervets use various behavioral strategies in their attempt to buffer themselves from environmental variability. During warmer periods, vervets spend significantly more time resting at the expense of feeding (McFarland et al. 2014). To reduce the effect of the heat, vervets also seek out shade, hug cool river rocks, retreat into aardvark burrows, and spend time swimming (Fig. 1). In cooler conditions, vervets can be seen sun-basking or huddling with other group members, as they try to maximize heat gain, or minimize heat-loss, respectively (Fig. 1). Vervets devote significantly more time to feeding, at the expense of resting, as part of their attempt to meet the energetic demands of colder conditions (McFarland et al. 2014).

So far, we have established that vervet monkeys in the Eastern Cape are more prone to cold stress than heat stress (Lubbe et al. 2014; McFarland et al. 2015; Henzi et al. 2017). Specifically, vervets display reduced thermoregulatory efficiency, experiencing lower, and increasingly hypothermic body temperatures, when temperatures are cold (i.e., the winter months). Moreover, we also see the greatest inter-individual variability in thermal competence at this time of year, and these effects become more pronounced as winter progresses and the energetic demands persist. The challenge of the cold is to minimize heat-loss to the environment whilst maximizing heat-gain and energy consumption. These problems are exacerbated at night, when vervets retreat to the trees and the risk of predation from land predators is highest (such predators present a significant risk at our study site, where vervets are exposed to black-backed jackal (*Canis mesomelas*), caracal (*Caracal caracal*) and several birds of prey: Pasternak et al. 2013; Ducheminsky et al. 2014). With minimal foraging capability, there is little a monkey can do to buffer itself against cold night-time temperatures. The only strategy available is to find another group member, and engage in huddling. Nocturnal huddling has been observed to be an important adaptation to a range of primate species living in temperate climates (Takahashi 1997;

Ogawa & Takahashi 2003; Li et al. 2010; McFarland & Majolo 2013). In line with these previous findings, our study has shown that thermal competence is positively predicted by an individual's number of social partners (McFarland et al. 2015; Henzi et al. 2017); a finding we interpret as reflecting variation in the number of potential huddling partners an animal can call on in cold temperatures. Interestingly, for males, we also found that their tenure length in the troop explains some of the variance in thermoregulatory competence. This suggests that learning and selecting suitable microhabitats at night may also play a role in improving thermoregulatory efficiency (Henzi et al. 2017). In a tangential experimental study of the heat-transfer characteristics of vervet monkey pelts, we found that grooming behavior (Fig. 1) apparently minimizes heat loss by increasing the pelt's insulative properties (i.e., loft), thus enabling animals to compensate for moderate environmental cooling, without increasing the demand of their metabolism (McFarland et al. 2016).

During hot conditions, vervets show remarkable efficiency in keeping their body temperature stable, and avoid significant bouts of hyperthermia (Lubbe et al. 2014). It is not surprising that vervets cope better with heat given that, as noted above, they have more strategies for dissipating heat than conserving it. In addition to bio-logging the vervets' temperature, we also use the same logging technology to measure environmental temperatures, and have found that, when vervets seek shade during the hottest part of the day, they select microclimates that can be up to twenty degrees cooler than direct exposure to the sun. Importantly, our vervets also have regular access to drinking water, which facilitates the sweat production necessary to dissipate heat in these conditions. Although largely a water-dependent species – vervets' geographical distribution is restricted to riverine habitats or artificial water sources maintained by humans – vervets can show remarkable resilience to periods of water unavailability, a circumstance not uncommon within their semi-arid, drought prone habitats. Prior to the beginning of our thermoregulation study (and partly the impetus for it), the vervets experienced a period of intense drought, during which there was very little free-standing water present in the troops' territories (McDougall et al. 2010). As a consequence, there was a marked increase in aggression over access to the little water that was present, despite these being small seepage points that offered little reward. More interesting, however, is what happened at the point when all free-standing water dried up completely. One of our troops was observed to leave their territory on the day after all the free-standing water dried up, venturing away from the river, along an exposed ridge unoccupied by any other vervet troops. They then returned to the river approximately 750m from their territory boundary, bypassing the ranges of four other groups, and entering an area containing a series of large pools. Our supposition is that the animals were led there by a male immigrant returning to his former territory. The willingness of other group members to follow this male, along with the intense aggression over largely unproductive water sources, suggests that vervets perceive direct access to water as crucial. In another of our groups, the loss of standing water did not prompt immediate movement in search of water. Instead, the group persisted without water for over a month by targeting succulent plants and licking dew from rocks and grass. Eventually, this group similarly followed an immigrant male to the water outside of their home territory. Visits by the two troops were then both regular and frequent, and the monkeys finally began sleeping at the new site. During this period, we observed no drought-related deaths, but it is clear that, had the monkeys not discovered a source of free-standing water, their survival would have been compromised. In this respect, the ability to observe and copy the behavior of animals with a broader experience of the surrounding area reflects another benefit of sociality.

Understanding how social influences on thermoregulation tie into vervet social dynamics is a topic we are now exploring in more detail. The Samara vervets display some interesting differences in their social behavior compared to the classic studies from Amboseli, which may be related to larger group sizes at our site (Henzi et al. 2013). Specifically, Samara females show clear grooming and proximity preferences for certain individuals, but these patterns are not easily explained by the standard organizing principles of rank and kinship: our females do not groom up the hierarchy, nor do they favor adjacently ranked females (i.e., those who are likely to be kin). There is no relationship between females' spatial proximity to each other and their probability of grooming (i.e., females do not simply groom whichever animal happens to be convenient). We have, however, shown that females use grooming strategically to secure safe spatial positions within the group: animals with larger grooming networks were less exposed to predation risk, from which they benefitted both reduced vigilance and increased foraging time (Josephs et al. 2016). It is also apparent, however, that there are large fluctuations in group size over time at our site, which reflect variation in climatic conditions—periods of drought result in increased rates of adult and infant mortality—and social patterns may thus vary accordingly. It may be that female social strategies vary in accordance with both group size and prevailing environmental conditions to produce cyclical patterns of variation over time: a possibility our long-term data will allow us to investigate more thoroughly.

To date, the adaptive value of sociability among primates has often been attributed to more sociable individuals being better able to deal with chronic social stress, which has a positive impact on reproduction (Silk 2007; Brent et al. 2013). Collectively, our research on vervets suggests that climatic variability can also present a significant source of stress to primate groups, and that more sociable individuals are better equipped to deal with such challenges. If more sociable animals are better able to minimize the metabolic costs of thermoregulation, it is probable that they are not only more likely to survive extreme environmental events, but these savings in maintenance costs mean they also have more energy to invest in reproduction. Our work therefore contributes to the growing body of evidence suggesting that sociability and behavioral flexibility are evolutionarily adaptive traits, and are likely to play an important role in promoting the ongoing viability of populations living in highly-variable, extreme environmental conditions (Henzi et al. 2009; Henzi et al. 2013; McFarland & Majolo 2013; Young et al. 2014; McFarland et al. 2014, 2015; Young et al. 2017; Henzi et al. 2017; McFarland et al. 2017).

**References**

Brain C, Mitchell D. 1999. Body temperature changes in free-ranging baboons (*Papio hamadryas ursinus*) in the Namib Desert, Namibia. International Journal of Primatology 20: 585-598.

Brent LJ. et al. 2013. Genetic origins of social networks in rhesus macaques. Scientific Reports 3: 1042.

Campos FA, Fedigan LM. 2009. Behavioural adaptations to heat stress and water scarcity in white-faced capuchins (*Cebus capucinus*) in Santa Rosa National Park, Costa Rica. American Journal of Physical Anthropology 138: 101-111.

Dausmann KH, Glos J, Ganzhorn JU, Heldmaier G. 2004. Physiology: Hibernation in a tropical primate. Nature 429: 825-826.

Ducheminsky N, Henzi SP, Barrett L. 2014. Responses of vervet monkeys in large troops to terrestrial and aerial predator alarm calls. Behavioral Ecology 25: 1474-1484.

Dunbar RIM. 1991. Functional significance of social grooming in primates. Folia Primatologica 57: 121-131.

Estrada A, Garber PA, Rylands AB, Roos C, Fernandez-Duque E, Di Fiore A, Nekaris KAI, Nijman V, Heymann EW, Lambert JE, Rovero F. 2017. Impending extinction crisis of the world's primates: Why primates matter. Science Advances 3: e1600946.

Fuller A, Mitchell D, Maloney SK, Hetem RS. 2016. Towards a mechanistic understanding of the responses of large terrestrial mammals to heat and aridity associated with climate change. Climate Change Responses 3: 10.

Henzi SP, Hetem R, Fuller A, Maloney S, Young C, Mitchell D, Barrett L, McFarland R. 2017. Consequences of sex-specific sociability for thermoregulation in male vervet monkeys during winter. Journal of Zoology.

Henzi SP, Forshaw N, Boner R, Barrett L, Lusseau D. 2013. Scalar social dynamics in female vervet monkey cohorts. Philosophical Transactions of the Royal Society B: Biological Sciences, 368: 20120351.

Henzi SP, Lusseau D, Weingrill T, Van Schaik CP, Barrett, L. 2009. Cyclicity in the structure of female baboon social networks. Behavioral Ecology and Sociobiology 63: 1015-1021.

Hill RA, Barrett L, Gaynor D, Weingrill T, Dixon P, Payne H, Henzi SP. 2003. Day length, latitude and behavioural (in) flexibility in baboons (*Papio cynocephalus ursinus*). Behavioral Ecology and Sociobiology 53: 278-286.

Hoffman MT, Carrick PJ, Gillson L, West AG. 2009. Drought, climate change and vegetation response in the succulent karoo, South Africa. South African Journal of Science 105: 54–60.

Josephs N, Bonnell T, Dostie M, Barrett L, Henzi SP. 2016. Working the crowd: sociable vervets benefit by reducing exposure to risk. Behavioral Ecology 27: 988–994.

Korstjens AH, Lehmann J, Dunbar RIM. 2010. Resting time as an ecological constraint on primate biogeography. Animal Behaviour 79: 361-374.

Li D, Ren B, Grueter CC, Li B, Li M. 2010. Nocturnal sleeping habits of the Yunnan snub-nosed monkey in Xiangguqing, China. American Journal of Primatology 72: 1092-1099.

Lubbe A, Hetem RS, McFarland R, Barrett L, Henzi SP, Mitchell D, Meyer LCR, Maloney SK, Fuller A. 2014. Thermoregulatory plasticity in free-ranging vervet monkeys, *Chlorocebus pygerythrus*. Journal of Comparative Physiology B 184: 799-809.

Majolo B, McFarland R, Young C, Qarro M. 2013. The effect of climatic factors on the activity budgets of a temperate primate, the Barbary macaque (*Macaca sylvanus*). International Journal of Primatology 34: 500-514.

Maslin MA, Shultz S, Trauth MH. 2015. A synthesis of the theories and concepts of early human evolution. Philosophical Transactions of the Royal Society of London B: Biological Sciences 370: 20140064.

McDougall P, Forshaw N, Barrett L, Henzi SP. 2010. Leaving home: Responses to water depletion by vervet monkeys. Journal of Arid Environments 74: 924-927.

McFarland R, Murphy D, Lusseau D, Henzi SP, Parker JL, Pollet TV, Barrett L. 2017. The ‘strength of weak ties’ among female baboons: fitness-related benefits of social bonds. Animal Behaviour.

McFarland R, Henzi SP, Barrett L, Wanigaratne A, Coetzee E, Fuller A, Hetem RS, Mitchell D, Maloney SK. 2016. Thermal consequences of increased pelt loft infer an additional utilitarian function for grooming. American Journal of Primatology 78: 456-461.

McFarland R, Fuller A, Hetem RS, Mitchell D, Maloney SK, Henzi SP, Barrett L. 2015. Social integration confers thermal benefits in a gregarious primate. Journal of Animal Ecology 84: 871-878.

McFarland R, Barrett L, Boner R, Freeman NJ, Henzi SP. 2014. Behavioral flexibility of vervet monkeys in response to climatic and social variability. American Journal of Physical Anthropology 154: 357-364.

McFarland R, Hetem RS, Fuller A, Mitchell D, Henzi SP, Barrett L. 2013. Assessing the reliability of biologger techniques to measure activity in a free-ranging primate. Animal Behaviour 85: 861-866.

McFarland R, Majolo B. 2013. Coping with the cold: Predictors of survival in wild Barbary macaques, *Macaca sylvanus*. Biology Letters 9: 20130428.

Mzilikazi N, Masters JC, Lovegrove BG. 2006. Lack of torpor in free-ranging southern lesser galagos, Galago moholi: Ecological and physiological considerations. Folia Primatologica 77: 465-476.

Nowack J, Mzilikazi N, Dausmann KH. 2010. Torpor on Demand: Heterothermy in the Non-Lemur Primate Galago moholi. PLoS ONE 5: e10797.

Ogawa H, Takahashi H. 2003. Triadic positions of Tibetan macaques huddling at a sleeping site. International Journal of Primatology 24: 591-606.

Pasternak G, Brown LR, Kienzle S, Fuller A, Barrett L, Henzi SP. 2013. Population ecology of vervet monkeys in a high latitude, semi-arid riparian woodland. Koedoe 55: 1-9.

Potts R. 1998. Variability selection in hominid evolution. Evolutionary Anthropology: Issues, News, and Reviews 7: 81-96.

Schülke O, Bhagavatula J, Vigilant L, Ostner J. 2010 Social bonds enhance reproductive success in male macaques. Current Biology 20: 2207-2210.

Silk JB. 2007. The adaptive value of sociality in mammalian groups. Philosophical Transactions of the Royal Society B 362: 539-559.

Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM, Seyfarth RM, Cheney DL. 2009 The benefits of social capital: close social bonds among female baboons enhance offspring survival. Proceedings of the Royal Society B 276: 3099-3104.

Takahashi H. 1997. Huddling relationships in night sleeping groups among wild Japanese macaques in Kinkazan Island during winter. Primates 38: 57-68.

Thomas CD et al. 2004. Extinction risk from climate change. Nature 427: 145-148.

Thompson CL, Williams SH, Glander KE, Teaford MF, Vinyard CJ. 2014. Body temperature and thermal environment in a generalized arboreal anthropoid, wild mantled howling monkeys (*Alouatta palliata*). American Journal of Physical Anthropology 154: 1-10.

Wiederholt R, Post E. 2010. Tropical warming and the dynamics of endangered primates. Biology Letters 6: 257-260.

Young C, Majolo B, Heistermann M, Schülke O, Ostner J. 2014. Responses to social and environmental stress are attenuated by strong male bonds in wild macaques. Proceedings of the National Academy of Sciences 111: 18195-18200.

Young C, McFarland R, Barrett L, Henzi SP. 2017. Formidable females and the power trajectories of socially integrated male vervet monkeys. Animal Behaviour 125: 61-67.

**Figure legends**

Figure 1. Behavioral responses of wild vervet monkeys to climatic variability.

*left to right: drinking, swimming, rock-hugging, resting in shade, grooming, feeding, huddling, and sun-basking.