Social integration confers thermal benefits in a gregarious primate

Richard McFarland[a,b*], Andrea Fuller[a], Robyn S Hetem[a], Duncan Mitchell[a,c], Shane K Maloney[a,c], S Peter Henzi[d,e], Louise Barrett[a,d]

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

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

[c]School of Anatomy, Physiology and Human Biology, University of Western Australia, Australia

[d]Department of Psychology, University of Lethbridge, Canada

[e]Applied Behavioural Ecology & Ecosystems Research Unit, University of South Africa, South Africa

***Corresponding author**: [b]Department of Anthropology, 1180 Observatory Drive, University of Wisconsin-Madison, Madison, WI 53706, United States

Running headline: Sociable monkeys are better thermoregulators

Summary

1. Sociality has been shown to have adaptive value for gregarious species, with more socially integrated animals within groups experiencing higher reproductive success and longevity. The value of social integration is often suggested to derive from an improved ability to deal with social stress within a group; other potential stressors have received less attention.
2. We investigated the relationship between environmental temperature, an important non-social stressor, and social integration in wild female vervet monkeys (*Chlorocebus pygerythrus*), using implanted data-loggers to obtain direct measures of core body temperature.
3. Heterothermy (as measured by 24h amplitude of body temperature) increased, and 24h minima of body temperature decreased, as the 24h minimum ambient temperature decreased. As winter progressed, monkeys became increasingly heterothermic and displayed lower 24h minima of body temperature.
4. Monkeys with a greater number of social partners displayed a smaller 24h amplitude (that is, were more homeothermic) and higher 24h minima of body temperature (that is, became less hypothermic), than did animals with fewer social partners.
5. Our findings demonstrate that social integration has a direct influence on thermoregulatory ability: individual animals that form and maintain more social relationships within their group experience improved thermal competence compared to those with fewer social relationships.

6. Given the likely energetic consequences of thermal benefits, our findings offer a viable physiological explanation that can help account for variations in fitness in relation to individual differences in social integration.

Key words: body temperature, cold stress, primates, sociality, thermoregulation, vervet monkeys

Introduction

There is growing evidence to suggest that, among a variety of mammals, the number and strength of social bonds between animals is positively correlated with both reproductive success and longevity, and hence to individual fitness benefits (Armitage & Schwartz 2000; Silk, Alberts & Altmann 2003; Smith & Christakis 2008; Weidt, Hofmann & König 2008; Cameron, Setsaas & Linklater 2009; Silk et al. 2010; Schülke et al. 2010; Frère et al. 2010). The physiological underpinnings of this relationship have been explored in humans (Berkman & Glass 2000; Smith & Christakis 2008), but such work is only just beginning for other species. Among non-human primates, the benefit of increased social integration has been argued to derive from an improved ability to deal with 'social stress', based on findings demonstrating that females with strong social bonds display lower glucocorticoid levels than do females with weaker bonds (Crockford et al. 2008; Silk et al. 2010; Brent et al. 2011). Chronic elevated stress can have negative effects on fertility (Cameron 1997; Tamashiro, Nguyen & Sakai 2005) and immunity (Cohen et al. 1992, 1997), and this is thought to explain why female primates that maintain strong and stable social bonds experience improved reproductive success (Silk et al. 2003; Silk et al. 2009).

One recent study of Barbary macaques (*Macaca sylvanus*), however, provides suggestive evidence of a different kind of link between social integration and fitness: animals with a greater number of social partners were more likely to survive an extremely cold winter than were those with fewer social partners (McFarland & Majolo 2013). One possible explanation for these results is that surviving animals were able to more effectively maintain their body temperature within an acceptable range, and did so because they were afforded greater opportunities for huddling, particularly at night (when diurnal animals are less active), which reduces heat loss and energy expenditure in the cold (Satinoff 2011). Moreover, the availability of alternative social partners that could replace those who perished may have provided more consistent opportunities for huddling across the winter. Such behavioural responses are likely to be employed in the cold because autonomic processes that can be used to defend core body temperature are energetically costly such that, where possible, endotherms should prefer less costly changes in behaviour, like microclimate selection, to sustain homeothermy (i.e., regulating their body temperature within a narrow range). One obvious way in which social animals, in particular, can influence their microclimate is to huddle (e.g., Nuñez-Villegas, Bozinovic & Sabat 2014). A more detailed examination of the thermal benefits that animals derive from social relationships may therefore augment and enhance our understanding of the link between fitness and sociality, and also provide a mechanism by which social animals can buffer the effects of environmental stress.

To address this issue, we have been studying a wild vervet monkey population (*Chlorocebus pygerythrus*), a gracile cercopithecine with a wide latitudinal distribution in Africa, with the aim of understanding how the effects of the thermal environment are mediated by social engagement. Here, we test whether the ability of animals to maintain their body temperature is systematically related to individual variation in their level of social integration. Specifically, we examine variation in the body temperature (quantified as the 24h amplitude, minima, maxima and mean) of female monkeys across the austral winter in relation to social bond status, predicting that animals with more social bonds will show improved thermoregulatory ability. Previous work on our population has established that our animals experience cold stress rather than heat stress (Lubbe et al. 2014), with greater individual variation in homeothermy during the winter months, hence our focus on the winter period. As bond strength as well as number of associates have been shown to provide fitness benefits in primates (Silk et al. 2003; Silk et al. 2010; Schülke et al. 2010; McFarland & Majolo 2013), we also tested whether animals with stronger bonds regulated their body temperature within a narrower 24h range. In order to assess the possibility that any observed differences in thermal competence were mediated by socially enhanced food intake, we also analysed feeding time in relation to the number of social partners.

Methods

Data were collected between January 2011 and August 2012 from two groups of wild vervet monkey in the Eastern Cape, South Africa (32^{o}22'S, 24^{o}52'E). These animals feed on a completely natural diet, are fully habituated to the presence of researchers, and can be individually identified by means of natural markings (Pasternak et al. 2013; McFarland et al. 2014).

Body temperature

Twelve adult females were implanted abdominally with temperature data loggers, which recorded core body temperature at five-minute intervals. Monkeys were immobilized using blow-darts filled with a combination of midazolam (2.5 mg: Roche Products, Isando, South Africa) and ketamine (50 mg: Bayer, Isando, South Africa). Following recumbence (approximately 5 min), monkeys were transported to a temporary operating theatre within 5 km of their home range. Prior to surgery, monkeys were injected intramuscularly with an antibiotic (Peni LA: 0.1 ml/kg) and anti-inflammatory (Carprofen: 3 mg/kg, Pfizer Laboratories, Sandton, South Africa), and injected subcutaneously at the incision site with a local anaesthetic (Lignocaine: 40 mg/animal, Bayer). Animals were intubated and anaesthesia was maintained (0-2% isoflurane in oxygen: Isofor, Astra Zeneca Pharmaceuticals, Johannesburg, South Africa). In preparation for surgery, a 100x100mm region of the abdominal surface was shaved and sterilized using chlorhexidine (Hibicol, Kyron Laboratories, Benrose, South Africa). Eye ointment was used to keep the monkeys' eyes moist (Terra-Cortril: Pfizer Laboratories) and electric blankets were used to reduce the risk of hypothermia. Prior to implantation, data loggers were coated in inert wax and dry-sterilized in formaldehyde vapour (Sasol wax 1276; Sasol, South Africa) for waterproofing and sterilization respectively (total data logger mass: approximately 25g, <1% body mass). Data loggers were implanted in the abdomen via an incision made through the dermal layer and linea alba. During surgery, Ringers solution (B. Braun Medical, Northriding, South Africa) was administered at 1 drop/s. Arterial haemoglobin oxygen saturation, blood pressure, heart rate, rectal temperature and respiratory rate were monitored continuously throughout surgery. Following the completion of surgery, the incision site was sprayed with F10 germicidal wound spray (Health and Hygiene, Sunninghill, South Africa) and the monkeys were allowed to recover fully in cages before being released back into their group – approximately two hours after capture. Monkeys were observed daily thereafter to monitor the progress of their recovery. Normal behaviour resumed on the day after surgery and no monkeys were compromised as a result of surgery. After 12 months, the same procedure was used for the removal of data loggers. All capture and surgical procedures were approved by the University of the Witwatersrand Animal Ethics Screening Committee (clearance number AESC 2010/41/04) and conformed to the legal requirements of South Africa.

Behavioural and environmental data

Between January and August each year, instantaneous scan data (Altmann 1974) were collected daily from all group members. Scan data were collected from all adult/sub-adult group members located within a ten-minute time frame, every thirty minutes (mean ± SD = 360 ± 176 scans per implanted female each year). In addition to data on non-social activity (resting, moving, foraging), we recorded whether the monkeys were grooming or within 2m of another group member. The identities of all grooming partners and animals in close proximity were recorded. See Henzi et al. (2013) for more detail on the general patterns of affiliation observed in our study population. Behavioural data collection protocols were approved by the University of Lethbridge under the terms of reference of Animal Welfare Protocol 0702.

Behavioural data were used to calculate two measures of sociability: the number and mean strength of social relationships a female shared with other group members. The number of social relationships a female had was defined as the number of group members with which she had been observed to exchange grooming at least once during scan sampling. Fig. S1 shows the distribution of the number of social relationships across our study population. A composite sociality index (CSI: see Silk et al. 2009) was used to measure the mean strength of the social bonds each female held in her group (McFarland & Majolo 2013):

$$\mathrm{CSI} = \frac{\sum_{i=1}^{2} \frac{x_i}{m_i}}{2}$$

Two dyadic behavioural measures were entered into the CSI: the proportion of scans that each dyad was (i) grooming and (ii) not grooming but within 2m. These two variables had similar variance (SDs = 0.02 and 0.07, respectively) and were significantly positively correlated ($P<0.001$, Appendix 1). We entered proportional values into this index to control for the fact that some individuals were scanned more frequently than others. To control for the fact that not all monkeys were present in the study group for the same amount of time, these proportions were divided by the total number of months that the two members of the dyad co-resided in the group. These adjusted dyadic behavioural measures (x_i) were divided by the group's mean for these same measures (m_i). These values were summed across all group member dyads, and divided by two; the number of behavioural measures entered into the index. By definition, the mean CSI is one, but can range from zero to infinity. To calculate the mean strength of the social bonds a female shared in their group, we summed the CSI scores for each female and divided this value by the total size of their group. Fig. S2 shows the distribution of CSI scores across our study population.

It should be noted that the distribution of our subjects across troops and years precluded the construction of a reliable unitary measure of dominance rank that could be used in our analysis. This is relevant because the number of other females with which a given female associates potentially could be linked to her dominance rank. A series of separate analyses conducted across a five-year period, however, indicate that there is no relationship between a female's rank and the number of her associates in our population (Henzi et al. 2013; Matlock 2013; Josephs unpublished data). Hence, any effect of rank on thermoregulation is unlikely to be due to a simple confound between a female's social status and the number of females with which she associates. Black globe (i.e. ambient) temperature was recorded on site at a local weather station. Nocturnal winter air temperatures fell as low as -4°C (mean minima ± SD = 1.8 ± 3.6°C).

Statistical analysis

We analysed body temperature data collected across two winters (i.e. June through August). We ran four linear mixed models (LMMs), entering either daily measures of (i) 24h amplitude, (ii) minimum, (iii) maximum and (iv) mean body temperature in turn as the dependent variable. Minimum daily ambient temperature, number of social partners, mean bond strength and consecutive day of the winter (i.e. 1 - 92), were entered as independent variables. Body mass and group ID were entered as control variables. Year, nested inside subject ID, was entered as a random factor. We ran a final LMM with the proportion of the activity spent feeding as the dependent variable. We applied an arcsine transformation to this variable to improve normality of this data. The number of social partners was entered as the independent variable. Group ID was entered as a control variable. Year, nested inside subject ID, was entered as a random factor. All models were run in STATA statistical software (Statacorp 2013). All model residuals met the modelling assumptions of LMMs with normal error structure.

Results

The 24h minimum ambient temperature was correlated negatively with the 24h amplitude of body temperature, correlated positively with the 24h minimum and mean body temperature, and was unrelated to the 24h maximum body temperature of the monkeys (Table 1). Fig. 1 indicates that the monkeys reached their minimum 24h body temperatures between sunset and sunrise. As winter progressed (i.e., day of winter increased), monkeys showed significantly higher 24h amplitudes of body temperature (Fig. 2a), and significantly lower 24h minimum (Fig. 2b) and average body temperatures (Table 1). 24h maximum body temperature was correlated positively with the day of winter (Table 1).

While controlling for minimum ambient temperature and the day of winter, monkeys with more social partners were less heterothermic. The number of social partners per individual was correlated negatively with the 24h amplitude of body temperature (Fig. 3a), correlated positively with the 24h minimum body temperature (Fig. 3b), but was not correlated with either the 24h maximum or 24h mean body temperatures (Table 1). Figure 4 provides an illustrative example of this general effect by displaying the body temperature patterns of the females with the most and fewest social partners, on a cold winter’s night. The mean bond strength of an individual monkey was not correlated with the 24h amplitude of body temperature, or the 24h minimum, maximum or mean body temperature (Table 1).

We found no relationship between the number of a female's social partners and the proportion of time females spent feeding (Z=-0.19, P=0.85, β±SE=-0.001±0.004, N=14).

Discussion

Our results show that female vervet monkeys were compromised thermally by low nocturnal ambient temperatures, and became increasingly heterothermic (i.e., displayed a larger amplitude of 24h body temperature) as winter progressed. As predicted, females with more social partners fared better than those with fewer partners.

The link between social integration and thermoregulatory advantage suggests that behavioural adjustment of their microclimates via the presence of other tolerant animals is the mechanism underlying our result. More specifically, it seems likely that huddling during the night, when animals are constrained into being less active, accounts for the differential thermal consequences of variable sociability. Nocturnal huddling has been observed in a range of primate species, including vervet monkeys (Takahashi 1997; Ogawa & Takahashi 2003; Li et al. 2010; McFarland & Majolo 2013; Danzy et al. 2014). Although the ability of small primates to use burrows or nest holes may negate the benefits of huddling (Dausmann & Glos, in press), for those that cannot use burrows or nest holes, huddling reduces heat loss and thereby the heat production required to maintain core body temperature (Gilbert et al. 2010). Vervet monkeys do not enter torpor as a means to conserve energy, so the energy demand of maintaining homeothermy in the cold is likely to be greater for an individual monkey that is unable to huddle. The most effective huddling is likely to involve several individuals that cluster together, with the best position being between two or more individuals (Bustamante, Nespolo & Rezende 2002; Gilbert et al. 2010; Nuñez-Villegas, Bozinovic & Sabat 2014). Having more social partners may either allow for the formation of bigger huddling groups, make it easier for a monkey to find a huddling partner, or both. If a specific partner is unavailable, an individual monkey with fewer social partners might remain alone. Macaques appear to choose their nocturnal huddling partners according to diurnal levels of affiliation (Takahashi 1997; Ogawa & Takahashi 2003). If this were a general trend, a monkey's ability to use huddling to aid thermoregulation would be highly dependent on its ability to maintain a network of social relations. Clearly, although our results are consistent with this hypothesis, the link between social integration and huddling partner availability remains speculative for the moment. We are, however, collecting data on huddling during night-time hours to provide a more definitive test.

Previous primate studies linking measures of social integration to female fitness have tended to focus on the importance of maintaining a small, focused network of very strong and stable social bonds (e.g., Silk et al. 2003; Silk et al. 2009; Brent et al. 2011). These studies suggest that animals with consistent access to 'social support' are likely to deal better with social stress, and that this has a positive impact on female reproductive success. In contrast, our results indicate that, in response to environmental stress, the crucial element is the number of partners on which an individual can call, rather than on the strength or 'quality' of the relationship that she has with particular companions. In other words, no simple quantity-quality trade-off exists: fewer, stronger bonds will not necessarily compensate for a greater number of weaker bonds in reducing thermoregulatory costs in cold conditions. In this regard, the benefits of retaining broad integration within the network of the group may counter any tendency for animals to form smaller mutualistic sub-units, thereby also preserving group coherence across time. Together, these findings suggest that under different selective pressures, different features of social integration are likely to have a differential impact on individual fitness.

One might argue that more socially integrated monkeys performed better in the cold because they consumed more food during the day – due to the improved feeding tolerance associated with social relationships – and thus had more energy available for metabolic thermogenesis at night. The absence of a relationship between the number of social partners and the amount of time a female spent feeding, however, lends support to the notion that the thermal benefit of sociability is mediated by social thermoregulation, not socially enhanced food intake. It is possible, however, that animals with more social partners have better access to higher quality food resources, and experience reduced competition when feeding; both of which may carry energetic benefits. The inclusion of body mass in our analyses may control to some extent for the effect of inter-individual variability in the nutritional benefits afforded by socially enhanced food intake. Nonetheless, further investigation into whether social integration has a significant effect on the interplay between energy intake and expenditure will improve our understanding of the relationship between social integration and thermal efficiency.

Female monkeys that are better able to reduce the metabolic costs of maintaining homeothermy potentially could invest more energy in reproduction, reproduce at a faster rate, and either directly (through maternal investment) or indirectly (as their offspring would receive similar benefits) increase infant survival. In extreme environments, individual monkeys more effective at conserving energy would also be more likely to survive. Thermal benefits mediated by social relationships may thus represent an important component of the positive relationship between social integration and fitness. That is, the direct thermal and energetic benefits that social integration confers may be at least as important as the stress-buffering effects suggested previously (Crockford et al. 2008; Silk et al. 2010; Brent et al. 2011). Stress buffering is argued to operate as it does in humans (i.e., by attenuating the increased levels of physiological and psychological stress associated with social isolation), as well as potentially providing protection from social harassment and increasing access to nutritional resources (Silk et al. 2003). Our results, however, lead us to suggest an additional, more direct route by which social integration can have an impact on fitness, with direct energy savings accruing as a result of physical contact with others. For *Chlorocebus*, this impact is likely to be felt surprisingly widely. Populations in at least three of the six constituent taxa experience the same mean 24h minimum monthly temperatures that our animals do, and the <6°C isotherm encloses 9.4% of the genus's range (Fig. 5). For vervets, in particular, with their large latitudinal distribution, this rises to 19.4%, suggesting that there will be value in exploring in more detail the correlates and consequences of dealing with the cold.

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Data accessibility

Data are archived on figshare: http://dx.doi.org/10.6084/m9.figshare.1265056

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Figure legends

Fig. 1. Histogram showing the time of day the monkeys reached their minimum body temperatures

Fig. 2. Predictive margins with 95% CIs for the relationship between the number of days in to winter and (a) the amplitude and (b) the 24h minimum core body temperature of female vervet monkeys

Fig. 3. Predictive margins with 95% CIs for the relationship between the number of social partners and (a) the amplitude and (b) the 24h minimum core body temperature of female vervet monkeys

Fig. 4. An example of variation in body temperature patterns observed in the most (19 partners) and least social female (6 partners) on a cold winter's night

Fig. 5. The distribution of the *Chlorocebus* taxon group in Africa (hatching) in relation to regions experiencing mean 24h minimum monthly temperatures below 6°C (shaded). The distribution was compiled from IUCN Red List maps for each of the constituent taxa (2008. http://www.iucnredlist.org/). Temperature data were extracted from the WorldClim database at http://www.worldclim.org/ (see Hijmans et al. 2005). The black circle indicates the location of our study site.

Tables

Table 1. Results from the LMM analysis to test the effect of ambient temperature, sociability and day of winter on body temperatures

	β ± SE	***Z***	***P***
a) Amplitude in body temperature			
Minimum ambient temperature	-0.072 ± 0.005	-14.03	<0.001
Number of social partners	-0.030 ± 0.012	-2.45	0.01
Mean bond strength	-0.065 ± 0.171	-0.38	0.70
Day of winter	0.006 ± 0.001	8.57	<0.001
Body mass	0.688 ± 0.181	3.80	<0.001
Group	-0.474 ± 0.183	-2.58	0.01
Constant	1.214 ± 0.495	2.45	0.01
b) Minimum body temperature			
Minimum ambient temperature	0.070 ± 0.004	15.53	<0.001
Number of social partners	0.030 ± 0.010	3.00	<0.01
Mean bond strength	-0.148 ± 0.149	-0.99	0.32
Day of winter	0.005 ± 0.001	-7.39	<0.001
Body mass	-0.384 ± 0.173	-2.23	0.03
Group	0.283 ± 0.170	1.67	0.10
Constant	37.297 ± 0.478	77.95	<0.001
c) Maximum body temperature			
Minimum ambient temperature	0.002 ± 0.003	-0.76	0.45
Number of social partners	-0.007 ± 0.011	-0.65	0.51

Mean bond strength	-0.135 ± 0.152	-0.89	0.38
Day of winter	0.002 ± 0.000	4.37	<0.001
Body mass	0.256 ± 0.159	1.61	0.11
Group	-0.118 ± 0.162	-0.73	0.47
Constant	38.612 ± 0.434	89.07	<0.001
d) Average body temperature			
Minimum ambient temperature	0.027 ± 0.002	11.50	<0.001
Number of social partners	0.002 ± 0.006	0.32	0.75
Mean bond strength	-0.089 ± 0.092	-0.97	0.33
Day of winter	-0.001 ± 0.000	-2.92	<0.01
Body mass	-0.056 ± 0.113	-0.50	0.62
Group	0.069 ± 0.109	0.63	0.53
Constant	37.878 ± 0.314	120.58	<0.001

*****Analyses were run at the level of the subject/day. N=1047 from 12 monkeys.

Supporting Information

File name: Fig S1

Format: TIF

Description: Distribution of number of social partners.

File name: Fig S2

Format: TIF

Description: Distribution of sociality index values. CSI scores of zero (N=1005) are not presented in the figure.

File name: Appendix 1

Format: Word document

Description: Method and results for the LMM analyses of the relationship between the proportion of time dyads spent grooming and in close-proximity

File name: Graphical abstract

Format: jpg

Description: Graphical abstract