Consequences of sex-specific sociability for thermoregulation in male vervet monkeys during winter

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Abstract

Social integration underpins the ability of wild female vervet monkeys (*Chlorocebus pygerythrus*) to resist cold stress. Here we ask whether sociability is similarly salient for male vervet monkeys, who reside in non-natal groups as adults and who must consequently, therefore, develop social relationships on arrival. We use body temperature and social data from 15 free-ranging male vervet monkeys to determine whether the number of grooming partners is as important for them during winter and whether the length of residency is positively associated with body temperature. We also assess whether larger body size and higher dominance rank mitigate the need for social partnerships. Like females, male vervets respond to lower 24 h ambient temperatures and winter's progression by decreasing minimum and mean 24 h body temperatures and by becoming more heterothermic. Male rank had no effect, while body size was associated primarily with reduced heterothermy. Males with more social partners also sustained higher minimum and mean body temperatures but, unexpectedly, were consistently more heterothermic. Further analysis revealed that higher minimum and mean temperatures were a function of the number of female partners, while increased heterothermy was driven by the number of male partners. As winter and the mating season overlap, we interpret this as indicating that a need to sustain male associations incurs physiological stress that is reflected as a thermoregulatory cost. Lastly, we show that longer residency is associated with higher minimum body temperatures independently of social affiliation and suggest possible causes that might be investigated.

Keywords: body temperature, cold stress, primates, sociality, grooming

Introduction

While primates are generally considered a tropical clade [1], the distributions of a number of species incorporate high elevations or latitudes where individuals encounter severe winter climates [2–4]. The use of torpor, a temporary but substantial reduction in body temperature, can reduce energetic costs during exposure to cold or food scarcity for smaller primates [5] but, in larger species that do not employ torpor, there is evidence of significant thermoregulatory demands [6] that are not always sustainable [7], and for which socially-mediated thermoregulation offers at least a partial solution.

We have shown elsewhere that, under the thermal stress of very low nocturnal temperatures during the austral winter, female vervet monkeys (*Chlorocebus pygerythrus*) with more social partners were consistently more homeothermic and had higher nocturnal body temperatures than females with fewer social partners [8]. We attributed the tighter body temperature regulation to huddling [9], which is a common response by gregarious animals to low environmental temperatures [10–12], and the fact that access to more potential partners increases the possibility of having at least one other animal with which to huddle at night.

Our objective here is to extend this analysis to the thermal performance of male vervet monkeys in winter and to test the hypothesis that they will be, similarly, buffered against low environmental temperatures by the extent to which they are socially integrated. The primary reason for considering males separately is that they emigrate from their natal groups as adults and enter other groups as strangers, where they then reside for varying lengths of time [13]. This means, in effect, that they are obliged to establish new social contacts in each subsequent group; a process that will take time and which may, initially at least, preclude any significant reliance on other group members, especially if choice of huddling partners is biased towards kin [10]. To the extent to which social integration is important in male thermoregulation, it carries as a corollary the possibility that tenure length will be an important determinant of male thermal performance, with longer-term residents faring better than recent immigrants. We examine this question using the duration of residence of males in their current groups, and both the total number of social partners, and the number of partners of each sex that each male had. We do so because there is evidence that the benefits to males of social partners differ by sex and context [14]; [Young et al. in prep].

At the same time, adult males are almost twice the mass of females [15] with a consequent surface area to mass ratio that makes them intrinsically less vulnerable than adult females to short-term dry heat loss through conductance [16]. Therefore, while we expect individual body mass to be associated with thermoregulatory efficiency, as it is for females [8], we might also anticipate that being larger will reduce the reliance on social thermoregulation relative to that of females. Finally, we assess the relevance of male dominance rank for thermoregulation, expecting higher-ranking males to have priority of access to both food and to preferred microclimates, whether sleeping alone or as part of a huddle [17].

Material and methods

Study site and subjects

Data were collected between February 2012 and August 2014 from three groups of wild vervet monkey at Samara Game Reserve in the Eastern Cape, South Africa (32^{o}22’S, 24^{o}52’E), situated in the semi-arid karoo biome [15]. All study animals were fully habituated to the presence of researchers, could be identified individually by means of natural markings, and were reliant on natural sources of food and water [18]. The dates of immigration by males were recorded, allowing us to identify the body temperature patterns of males that were either recent immigrants, experiencing their first winter in their current groups (<12 months), or longer-term residents (>12 months). Black globe (i.e., ambient) temperature was recorded at an on-site weather station and ambient daily temperature profiles ranged from -5.2^{0}C to 42.5^{0}C .

Core body temperature data

Fifteen adult males (2012: N = 6, 2014: N = 9. Table 1) were implanted abdominally with temperature-sensitive data loggers, which recorded core body temperature at five-minute intervals across the two winters (Mean: 67 days ± 14SD/male/winter).

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 weighed to obtain body mass (Mean: 5.03 ± 0.57SD) and injected intramuscularly with an antibiotic (penicillin, Peni LA Phenix: 0.1 ml/kg) anti-inflammatory (carprofen, Rimadyl: 3 mg/kg, Pfizer Laboratories, Sandton, South Africa), and subcutaneously at the incision site with a local anaesthetic (lignocaine: 40 mg/animal, Bayer). The monkeys were intubated and anaesthesia was maintained using 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 gluconate in alcohol (Hibicol, Kyron Laboratories, Benrose, South Africa). Eye ointment kept the monkeys' eyes moist (hydrocortisone, Terra-Cortril: Pfizer Laboratories) and electric blankets were used to keep the animals warm.

Prior to implantation, the temperature 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, allowing the loggers to record accurate measurements of core-body temperature. During surgery, Ringers solution (B. Braun Medical, Northriding, South Africa) was administered via a drip at 1 drop/s. Arterial haemoglobin oxygen saturation, blood pressure, heart rate, rectal temperature and respiratory rate were monitored continuously throughout surgery.

After 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. The monkeys were monitored in the field to assess their recovery. Normal behaviour resumed on the day after surgery and no monkeys were compromised as a consequence 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.

Table 1

Behavioural data

Between February and August in both study years (viz. 2012 and 2014), instantaneous scan data [19] were collected daily, every thirty minutes, from all adult/sub-adult group members. Activity data (resting, moving, foraging or allo-grooming) were obtained from all visible group members over a 10-minute period. The identities of all grooming partners that were recorded during scans were used to determine the number of male (Mean: 4; Range: 0-9) and female (Mean: 5; Range: 0-10) partners that each male had groomed at least once, and these numbers were then combined to generate the total number of his adult grooming partners (Mean: 9; Range: 0-18).

Data were collected ad libitum on the occurrence of all dyadic agonistic interactions (e.g., displace, supplant, charge, chase, and physical contact). Agonistic data collected from males were used to construct group-specific male dominance hierarchies for the February-August study period in each of the two study years. A male's rank was expressed as a standardized normalized David's score [20]; [21], using the DomiCalc package ([22] in R 3.2.1 [23]]. It was not possible to record behavioural data blind because our study involved focal animals in the field. Behavioural data collection protocols were approved by the University of Lethbridge under the terms of reference of Animal Welfare Protocols 0702 and 1505.

Statistical analysis

We analysed body temperature data collected across the 2012 and 2014 winters (i.e., June through August). We ran four linear mixed models (LMMs), entering daily estimates of the (i) 24h minimum, (ii) 24h mean, (iii) 24h maximum and (iv) 24h amplitude of body temperature (i.e. maximum – minimum Tb) in turn as the response variable.

We entered minimum daily ambient temperature and consecutive day of the winter (i.e. 1 - 92) as control variables and the number of social partners, tenure length (expressed as presence or absence in the previous winter), standardized rank and body mass as explanatory variables. Analyses were run at the level of the subject/day, across two years (2012, 2014) and three groups. Subject ID nested inside Group ID, nested inside Year, was entered as a random factor. A random slope was specified only for minimum daily ambient temperature to enable the models to converge.

All LMMs were run in STATA statistical software [24]. Models were then corroborated in R, after which R^2s for the LMMs were generated using the MuMIn package [25]; where R^2_{MARGINAL} = the effect size of the fixed effects in the model and $R^2_{\text{CONDITIONAL}}$ = the effect size for the whole model [26]). Prior to running each model, we checked for multicollinearity by calculating variance inflation factors (VIF) for the predictor variables, excluding variables with VIFs > 4 [27]. Where appropriate, therefore, as indicated in the results, we used reduction in the Akaike Information Criterion (AIC) to estimate the relative likelihood of candidate models, with ΔAIC < -2.0 identifying a model with greater support than the alternative. As diagnostics, we evaluated the distributions of the response variables and the residuals of all models, and compared obtained standard errors to robust standard errors [28]. The models we present are those that best met the assumptions of normal error structure. Tests were two-tailed with $\alpha = 0.\ 05$.

Results

24- h minimum body temperature

The analysis provides evidence that the minimum T^0C increased with both the number of partners and the tenure length, while male dominance rank and body mass had no effect (Table 1. Figure 1a and Figure 2). Given high collinearity for the number of male and female partners (VIF>4), we ran model comparisons, entering each of the three measures of sociability (No. partners, No. males, No. females) separately to identify the strength of evidence for which, if either, of a male’s set of associates (male or female) were especially important in the determination of 24 h minimum body temperature. We held all other variables constant. The results indicate that the best performing model was the one run using No. Females, while the model with No. Males performed worst (No. Partners - No. Males: ΔAIC = -2.32; No. Females - No. Partners: ΔAIC = -2.28; No. Females - No. Males: ΔAIC = -4.60). Males with more female partners maintained higher minimum body temperatures.

Table 2

Figure 1

Figure 2

24 h mean body temperature

Mean body T^0C increased with the number of partners, while dominance rank, tenure length and body mass had no effect (Table 2). Model comparisons indicate that the best performing model was the one run using No. Females, while the model with No. Males performed worst (No. Partners - No. Males: ΔAIC = -2.48; No. Females - No. Partners: ΔAIC = -4.82; No. Females - No. Males: ΔAIC = -7.30). Males with more female partners maintained higher 24 h mean body temperatures.

Table 3

24 h maximum body temperature

None of the explanatory variables had an effect on maximum body temperature (Table 3).

Table 4

24 h amplitude of body temperature

The 24 h amplitude of body temperature was negatively associated with body mass and positively associated with the number of partners (Table 4. Figure 1b). Model comparisons provide no evidence for a difference between No. Males and No. Partners and 'considerably less empirical support' [29] than either of these for the model using No. Females (No. Partners - No. Males: ΔAIC = -0.69; No. Partners - No. Females: ΔAIC = -6.79; No. Males - No. Females: ΔAIC = -7.49). There is little to suggest that increases in the amplitude of body temperature were associated with the number of female partners.

Table 5

In models 1, 2 and 4, but not 3, the control variable, Days of winter, was significant and the pattern was a decrease in the 24 h minimum and mean body temperatures, and an increase in heterothermy (the 24 h amplitude of body temperature), as winter progressed, confirming that, as for females [8], there is a cumulative deleterious effect of winter on male body temperatures.

Discussion

Our results indicate that, in general terms, the patterns of male body temperatures during the taxing winter months at our study site resemble closely those of females from the same population [8]. Minimum and mean body temperature declined and heterothermy increased as winter progressed, suggesting an adaptive response to the increased energy demand associate with winter conditions [30]. An increase in body mass dampened the 24 h amplitude of body temperature but did not increase the 24 h minimum or mean body temperatures, while dominance rank had no effect on male body temperatures.

As for females, the primary buffer against cold for males was social, with the number of social partners allowing males to maintain minimum and mean body temperatures at levels similar to those seen in summer [6]. Interestingly, model selection indicates that these body temperature patterns were driven by the number of female grooming partners, with little evidence that body temperature control was augmented by the number of male partners, suggesting that males do not huddle with their male grooming partners. Given that females influence male dominance rank [Young et al. in prep.], with important consequences for mating opportunities [14], pursuing social integration with females is likely to be a strategic priority for male vervet monkeys for a number of reasons. In this context, with the number of partners accounted for in our models, the benefits of longer tenure for male thermoregulation cannot be ascribed to their associating with more females as their residency increases. There are at least two broad possibilities to explore: either that males become better at identifying sleeping sites with warmer microclimates or that they shift their social allegiance to females who do. The fact that their dominance rank plays no part lends some preliminary credence to the latter. Male reproductive success is contingent on female cooperation [31] and males are consequently reluctant to antagonise them. This reluctance underpins the effect of female association on male rank [Young et al. in prep.] and may well also apply here. Whereas a high ranking male might have little hesitation in evicting a solitary male from a preferred sleeping site, he is much less likely to do so to a male keeping company with females, especially during the mating season, which occurs during winter.

The co-occurrence of winter and the mating season is likely also to explain the unexpected and counter-intuitive finding that 24 h body temperature amplitude in males is positively associated with the number of social partners. For female vervets, having more partners was associated with higher minimum and mean body temperature and a smaller daily amplitude of body temperature [8]. While the number of female partners accomplishes the first two for males, it is likely that we are seeing the intersection of two conflicting social effects in respect of amplitude. Here, the amplitude-reducing influence of female partners, as reflected in the similarity of the models containing either male partners or males and females combined, is outweighed by the effects of an increasing number of male social partners, as reflected in the poor performance of the female partner-only model.

While grooming is usually considered a hedonic activity, with physiological benefits for both parties [32,33], and while male grooming partners are more likely to be coalition partners [14], our data point to the possibility that the maintenance of associations with an increasing number of males – who are reproductive competitors - is stressful and may present a disadvantageous physiological challenge for males with thermoregulatory consequences [34]. This outcome is then only partially offset by the benefits of associating with females, resulting in an increased 24 h amplitude of body temperature. We are currently analysing data on cortisol levels in males to assess more precisely the possibility that pursuing male social partners is stressful, and that any benefits to doing so are offset by its effects on male body temperature.

Compliance with ethical standards. All applicable institutional and national guidelines for the care and use of animals were followed.

Conflict of interest. The authors declare that they have no competing interests.

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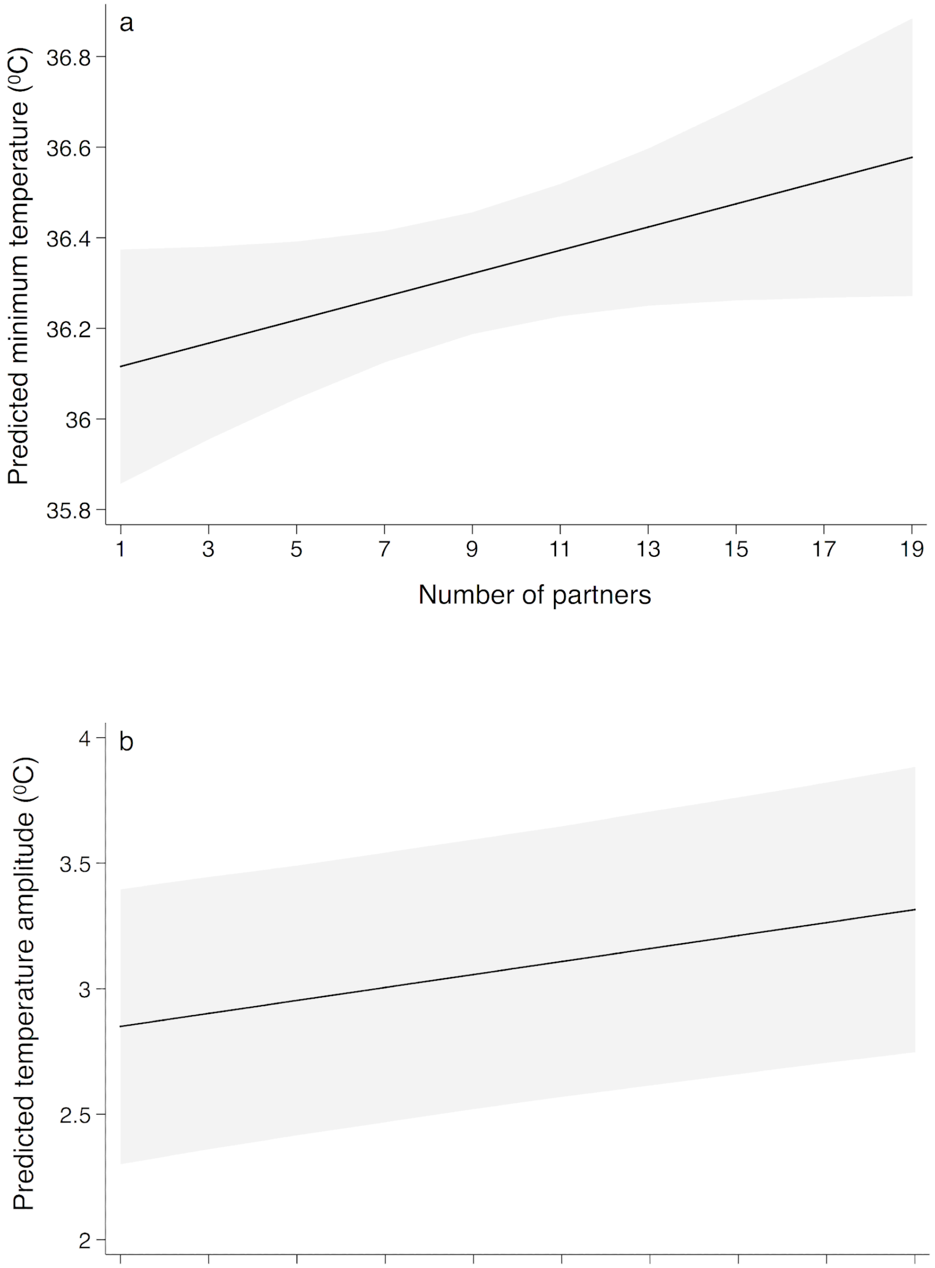

Figure 1. Predictive margins (± 95CI) for the relationship between the number of partners and (a) minimum body temperatures and (b) amplitude of body temperature for male vervet monkeys.

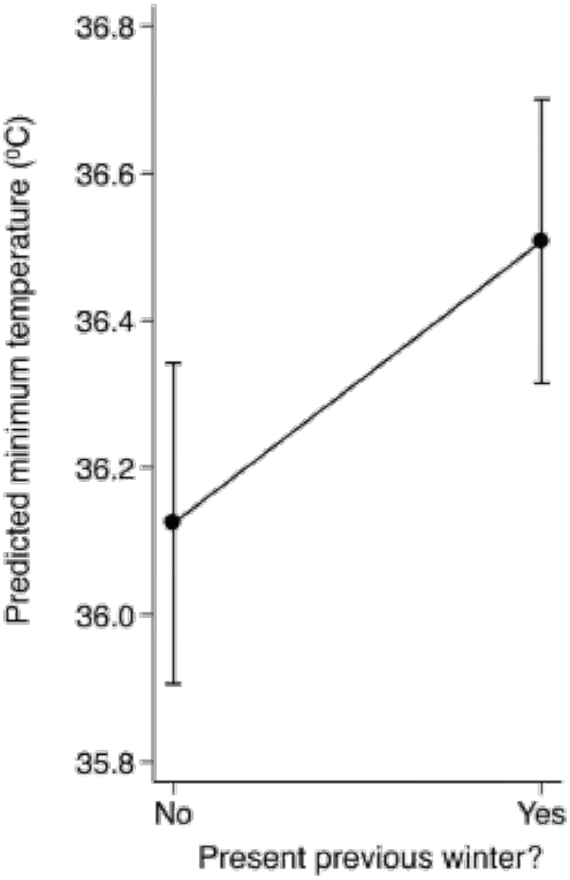

Figure 2. Predictive margins (± 95CI) for the relationship between male tenure length and minimum body temperatures.

Table 1. Details of the adult male vervet monkeys used as subjects. Number of days indicates the period during the austral winter for which we had body temperature data for each male. Body mass was that recorded at the time of surgery. Mean temperatures were calculated using relevant values for each 24-hr period across the winter. Absolute temperatures are the lowest and highest recorded from each male over the winter study periods.

ID	Year	No. days	Body mass	Mean T^0C	Mean min. T^0C	Mean max. T^0C	Abs min. T^0C	Abs max. T^0C
DA	2012	80	5.83	37.580	36.091	39.185	34.410	40.160
FL	2014	72	4.93	37.736	36.522	39.314	35.430	39.670
KE	2014	72	5.10	37.811	36.622	39.353	35.570	40.120
LG	2014	72	4.70	37.792	36.612	39.207	35.900	40.150
LE	2012	80	4.52	37.443	35.994	39.097	34.090	40.150
MC	2012	64	4.94	37.250	35.511	38.917	32.320	40.240
MJ	2012	54	3.62	37.670	36.125	39.344	34.830	40.230
MO	2014	72	5.10	37.980	36.907	39.458	36.010	40.150
OL	2012	33	5.23	37.882	36.566	39.305	35.270	39.710
PA	2014	72	5.41	37.877	36.675	39.252	35.640	39.640
RI	2014	72	4.43	37.686	36.282	39.161	35.230	39.540
ST	2012	43	5.86	37.489	35.961	39.257	34.120	39.870
TR	2014	72	5.00	37.622	36.352	39.103	35.430	39.610
UT	2012	80	5.49	37.599	35.774	39.566	33.920	40.230
ZO	2014	72	5.22	37.776	36.449	39.161	35.260	39.990

Table 2. Results from the linear mixed model to test the fixed effects of male rank, number of partners, tenure length, body mass on 24 h minimum body temperature in males. Day of winter and minimum 24 h ambient temperatures were entered as control variables and male identity, nested in group and year, was entered as a random effect, with a random slope specified for Minimum ambient T^0C. SE: standard error; CI: confidence intervals.

Variables	β	SE	Z	P	95 CI	
Male rank	0.146	0.178	0.820	0.411	-0.202	0.495
No. partners	0.028	0.014	1.990	0.047	0.000	0.055
Tenure length	0.368	0.156	2.360	0.018	0.062	0.674
Body mass	-0.121	0.124	-0.980	0.327	-0.363	0.121
Day of winter	-0.005	0.001	-6.150	0.000	-0.006	-0.003
Minimum ambient T^0C	0.062	0.008	7.860	0.000	0.046	0.077
intercept	36.499	0.630	57.910	0.000	35.264	37.734

Whole model: log likelihood = -745.287, Wald χ^2_6 = 119.430, P = 0.000. LR test vs linear model: Wald χ^2_4=150.570, $P < 0.0001$. $R^2_{MARGINAL} = 0.234$, $R^2_{CONDITIONAL} = 0.675$.

Table 3. Results from the linear mixed model to test the fixed effects of male rank, number of partners, tenure length, body mass on 24 h mean body temperature in males. Day of winter and minimum 24 h ambient temperatures were entered as control variables and male identity, nested in group and year, was entered as a random effect, with a random slope specified for Minimum ambient T^0C. SE: standard error; CI: confidence intervals.

Variables	β	SE	Z	P	95 CI	
Male rank	0.111	0.099	1.130	0.260	-0.082	0.305
No. partners	0.015	0.008	1.990	0.046	0.000	0.031
Tenure length	0.097	0.087	1.120	0.262	-0.073	0.267
Body mass	-0.028	0.069	-0.400	0.687	-0.162	0.107
Day of winter	-0.002	0.000	-5.680	0.000	-0.003	-0.002
Minimum ambient T^0C	0.019	0.002	7.820	0.000	0.015	0.024
intercept	37.657	0.350	107.480	0.000	36.970	38.344

Whole model: log likelihood = -165.543, Wald χ^2_6 = 108.50, P = 0.000. LR test vs linear model: Wald χ^2_4=144.480, P = 0.000. $R^2_{MARGINAL}$ = 0.150, $R^2_{CONDITIONAL}$ = 0.438.

Table 4. Results from the linear mixed model to test the fixed effects of male rank, number of partners, tenure length, body mass on 24 h maximum body temperature in males. Day of winter and minimum 24 h ambient temperatures were entered as control variables and male identity, nested in group and year, was entered as a random effect, with a random slope specified for Minimum ambient T^0C. SE: standard error; CI: confidence intervals.

Variables	β	SE	Z	P	95 CI	
Male rank	0.103	0.103	1.000	0.317	-0.099	0.306
No. partners	-0.001	0.008	-0.070	0.947	-0.016	0.015
Tenure length	0.040	0.091	0.450	0.656	-0.137	0.218
Body mass	0.023	0.072	0.320	0.747	-0.118	0.164
Day of winter	-0.001	0.000	-1.450	0.146	-0.002	0.000
Minimum ambient T^0C	-0.002	0.002	-1.070	0.286	-0.007	0.002
intercept	39.109	0.367	106.430	0.000	38.388	39.829

Whole model: log likelihood = -293.392, Wald χ^2_6 = 4.750, P = 0.000. LR test vs linear model: Wald χ^2_4=148.07, P = 0.000. $R^2_{MARGINAL}$ = 0.027, $R^2_{CONDITIONAL}$ = 0.373.

Table 5. Results from the linear mixed model to test the fixed effects of male rank, number of partners, tenure length, body mass on 24 h amplitude in body temperature. Day of winter and minimum 24 h ambient temperatures were entered as control variables and male identity, nested in group and year, was entered as a random effect, with a random slope specified for Minimum ambientT^0C. SE: standard error; CI: confidence intervals.

Variables	β	SE	Z	P	95 CI	
Male rank	-0.032	0.061	-0.520	0.604	-0.151	0.088
No. partners	0.026	0.008	3.110	0.002	0.010	0.042
Tenure length	-0.095	0.080	-1.190	0.234	-0.251	0.061
Body mass	-0.348	0.063	-5.550	0.000	-0.471	-0.225
Day of winter	0.004	0.001	4.990	0.000	0.002	0.005
Minimum ambient T^0C	-0.064	0.008	-7.710	0.000	-0.080	-0.048
intercept	4.598	0.384	11.980	0.000	3.846	5.350

Whole model: log likelihood = -787.305, Wald χ^2_6 = 160.52, P = 0.000. LR test vs linear model: Wald χ^2_4=134.92, P = 0.000. $R^2_{MARGINAL}$ = 0.245, $R^2_{CONDITIONAL}$ = 0.654.