Strategic (adaptive) hypothermia in bull dromedary camels during rut; could it increase reproductive success?

Gordon Grigg^{1,*}, Lyn Beard¹, Birgit Dörge², Jürgen Heucke², Jocelyn Coventry³, Alex Coppock⁴ and Simon Blomberg¹

¹School of Biological Sciences, University of Queensland, Queensland 4072, Australia

²Gutshof 2B, Lucklum 38173, Germany

³NT Department of Primary Industry, Fisheries and Mines, Alice Springs, Northern Territory 0870, Australia

⁴65 Elder Street, Alice Springs, Northern Territory 0870, Australia

*Author for correspondence (g.grigg@uq.edu.au).

In this study of body temperatures (T_b) in free ranging dromedary camels, we found that bulls in rut start the days cooler. Daily minima during rut averaged 0.6°C lower than at other times (95% CI 0.27 – 0.94°C) and daily maxima averaged 0.45°C higher (95% CI -0.01 to -0.91°C), increasing the daily T_b cycle. Knut Schmidt-Nielsen described a similar pattern in captive dromedaries deprived of water in hot conditions, which he interpreted as a strategy to conserve water. Our observations were made in winter and with water freely available. Dromedaries can apparently employ heterothermy for more than just water conservation. In the strenuous daily contests between rival bulls in rut, a lower T_b early in the day should extend the time for which a contestant can challenge or defend before heat stress becomes a problem. Calculations show that lowering T_b by even 0.6°C extends that time by more than 30 min, and many daily minima during rut were lower than that. Because the eventual winner of contests gains or retains a herd of females, we speculate that cooler T_b at the start of daily contests confers an advantage which translates directly into increased reproductive success.

Keywords: adaptive heterothermy; camels; rut; reproductive fitness

1. INTRODUCTION

Dromedary camels, *Camelus dromedarius*, are well known for adaptations to a desert existence, including tolerance to severe dehydration, ability to rehydrate rapidly when water is available, fat storage in the hump and tolerance of a wide range of body temperatures (T_b) (Wilson 1989). Their heterothermy was discovered by Schmidt-Nielsen *et al.* (1957), by measuring rectal temperatures of captive dromedaries in waterless, hot conditions. The camels tolerated T_b rising daily to 41 – 42°C , compared with 38°C when allowed access to water. Also, as if anticipating another challenging day ahead, they allowed T_b to cool

overnight, by radiation, to 34 – 35°C , lower than the normal 36°C . Daily ranges of 6°C or so in these hot, dry conditions contrasted markedly with normal daily cycles of approximately 2°C , representing considerable storage of heat above the (lowered) morning minimum T_b . This was interpreted as saving of water, which might otherwise been used for thermoregulation. The observations and their interpretation provided the seminal example of adaptive heterothermy (*sensu* Louw & Seely 1982) and have become a celebrated, textbook example of adaptation by a large mammal to hot dry deserts (e.g. Withers 1992).

We found a very similar pattern of daily heterothermy in dromedaries, but under completely different circumstances. We were attempting to discover experimentally whether the heterothermy described by Schmidt-Nielsen occurred in free-ranging camels, water-stressed in summer but free to employ normal thermoregulatory behaviours such as rest, shade seeking and choice of bodily orientation. Unusually wet conditions in the summers of 1998–1999 and 1999–2000 prevented us from prosecuting that study effectively because we could not deprive them of access to water. However, we uncovered instead a daily heterothermy very similar to the Schmidt-Nielsen pattern, not in response to hot dry conditions but in bull camels during rut.

2. MATERIAL AND METHODS

We worked between May 1998 and August 2000 on Newhaven, a cattle property 360 km northwest of Alice Springs in central Australia on the eastern edge of the Great Sandy Desert. A population of approximately 200 feral camels living in 20 000 ha bounded by salt lakes and a fence had been the subject of behavioural studies by two of us (Dörge & Heucke) for several years. Although wild, they had become habituated to humans and their histories and social positions were known. Some were confined in a 1600 ha paddock to enable closer tracking and observation. This paddock was large enough for normal behaviour (B. Dörge & J. Heucke 1986–1989 & 1996–2004, personal observations), was well vegetated with grasses and shrubs and had many trees for shade. Yards at one corner contained a water trough. Unusually high rainfall provided ephemeral water sources, but the camels chose often to drink from the trough.

Camels were trapped in the corner holding yards when they came to drink, usually as a herd. Four male and four female camels were used. Chosen individuals were manoeuvred into a specially designed race and anaesthetized by deep injection into the hind leg of a mixture of xylazine hydrochloride (100 mg ml^{-1} , 1.3 – 0.8 mg kg^{-1} IM Ilium Xylazil-100; Troy Laboratories, Australia) and ketamine hydrochloride (100 mg ml^{-1} , 1.3 – 0.8 mg kg^{-1} IM Ilium Ketamil injection; Troy Laboratories). Under this dissociative anaesthesia, we implanted custom-designed, calibrated temperature-sensitive radio-transmitters (Sirtrack Ltd, New Zealand) and calibrated data loggers (Gemini Data Loggers, UK) into the peritoneal cavity (Grigg & Beard 2001). The loggers collected T_b hourly for up to 10.5 months with an accuracy of $\pm 0.1^\circ\text{C}$. We also fitted longer range, radio-tracking collars (Sirtrack Ltd) for finding the camels within the study paddock. Anaesthesia was reversed using yohimbine hydrochloride (10 mg ml^{-1} , 0.5 – $1\text{ ml } 80\text{ kg}^{-1}$ IV Reversine injection; Parnell Laboratories, Australia) and 4-aminopyridine (24 mg ml^{-1} , 0.5 – $1\text{ ml } 80\text{ kg}^{-1}$ IV Xylex injection; Parnell Laboratories).

Data on daily T_b maxima and minima were analysed separately. Individuals were treated as random factors and data were analysed as repeated measures (rut versus non-rut) within each individual. Lack of independence in time-series data usually requires special methods to detect and model temporal correlations (Box *et al.* 1994). Plots of the autocorrelation and partial autocorrelation functions of the residuals for each individual in both the rut and non-rut periods showed little sign of temporal autocorrelation but, precautionarily, we fitted ARMA(2,2) models to the residuals of the data for each individual in the rut and non-rut periods using the nlme (nonlinear mixed effects) package for R (Pinheiro *et al.* 2007; R Development Core Team 2007).

Figure 1. Daily maximum and minimum body temperatures from approximately 10 months of data from each of four male camels plotted against the time of year. Inset: Daily cycles in body temperature in one of the bulls during 2000; note the increased daily ranges after mid-April when the animal was in rut. Filled circle, max; open triangle, min.

Table 1. Mean daily maximum and minimum body temperatures in four male camels over approximately 30 days in rut, compared with approximately 30 days not in rut. Daily cycles in T_b increased during the rut, a consequence of both lower daily minima and higher daily maxima.

	Herbie	005	Sputnik	Lumpi
<i>non-rut</i>				
$T_{b \text{ min}}$ (°C)	36.6	36.9	36.8	36.7
$T_{b \text{ max}}$ (°C)	37.7	37.8	37.9	37.8
range (°C)	1.1	0.9	1.1	1.1
period	1 Feb–2 Mar 2000	1 Feb–2 Mar 1999	1 Feb–2 Mar 2000	1 Feb–29 Feb 2000
<i>rut</i>				
$T_{b \text{ min}}$ (°C)	35.9	36.1	36.5	36.0
decrease (°C)	0.7	0.8	0.3	0.8
$T_{b \text{ max}}$ (°C)	38.5	38.2	38.6	37.7
increase (°C)	0.8	0.4	0.6	–0.1
range (°C)	2.5	2.1	2.0	1.7
period	15 Jun–15 Jul 2000	1 Jul–31 Jul 1998	24 Jul–24 Aug 2000	5 May–6 Jun 2000

3. RESULTS

Pronounced daily cycles of 0.5–3.3°C were seen routinely in all individuals (figure 1, table 1), as in captive camels (Wilson 1989). However, substantially larger daily cycles in T_b were observed in bull camels known from independent behavioural observation to be in rut. None coincided with hot conditions or water stress and, indeed, competing bulls often interrupted proceedings to drink (B. Dörgeres & J. Heucke 1998–2000, personal observations). Rut typically commences in early winter and lasts one to four months, even up to seven months, depending on the dominance of an individual (B. Dörgeres & J. Heucke 1986–1989 & 1996–2004, personal observations). Although rut is not synchronized completely, the overall pattern is sufficiently seasonal that pooling

all data from all male camels shows an obvious increase in daily temperature ranges between April and September (figure 1).

Exploring the data further, we compared 30-day periods when bulls were known to be in rut with 30-day periods when they were known not to be. Increased daily ranges in rut result from both lower daily minima and higher daily maxima (figure 2, table 1). The mean minimum T_b during rut was 0.60°C (s.e. = 0.11) lower than before entry to rut ($t_3 = -5.74$, $p = 0.01$) and the mean maximum 0.45°C (s.e. = 0.14) higher ($t_3 = 3.12$, $p = 0.052$), leading to an average increase in daily range in T_b from 1.04°C to 2.05°C (table 1). The intensity of the rut is not constant, so an average includes days with less activity as well as extremely competitive days;

Figure 2. Combined frequency histogram of daily maximum (open) and minimum (closed) body temperatures of four males during (a) rut and (b) non-rut sampling periods including and surrounding those identified in table 1 and for (c) four females during June and July (within male rut period); $n = 127, 121, 124$ (top to bottom).

averaging thus underestimates daily ranges associated with particularly intense contests. Nevertheless, there is almost no overlap between the lowest of the daily maxima and the highest of the minima for males in rut and non-rut periods (figure 2). Also, the lower $T_{b \text{ min}}$ in rutting males is not a consequence of lower ambient temperatures because females' T_b at the same time as the male rut period are equivalent to males when not in rut ($T_{b \text{ min}}$: $t_6 = 0.68$, $p = 0.52$; $T_{b \text{ max}}$: $t_6 = 1.56$, $p = 0.17$; figure 2). All four bulls won many contests and defended their herds of females throughout our study, except for Herbie who lost his in the last few days.

4. DISCUSSION

Fifty-two years after the publication of Schmidt-Nielsen *et al.* (1957), we describe a superficially similar pattern of heterothermy in camels, also driven significantly by lower daily minima, but occurring in quite different circumstances. It cannot be a strategy to save water; we saw it only in winter, only during rut and with water freely available and used routinely.

Is it adaptive and, if so, for what benefit? To be judged adaptive, the changed pattern should be of benefit to the camel and, also, should result from active regulation. Higher temperatures at the end of an active day could

be simply a consequence of the activity, but lowered T_b in the morning must be contrived, i.e. the result of active regulation. Schmidt-Nielsen also ascribed particular significance to his water-deprived camels lowering T_b in the morning, noting that the skin felt warm around dawn, presumably the result of active skin vasodilation.

In rut, competing bulls perform elaborate, ritualized and intense competitive behaviour including posing and strutting side by side, inflating and exposing the dulaa (a sac-like extension of the palate), jostling, exhibiting flehmen (curling upper lip to enhance chemoreception), running together and, not always but often, actually fighting. A bout ends when one bull admits defeat by leaving the scene. These behaviours persist for days and weeks, between the same or different contestants, and are very energetic; bulls lose body condition and sometimes die. The activity is mostly diurnal. T_b rises all day from the strenuous behaviour and the animals recuperate somewhat overnight, including lowering T_b . Triumph over rival bulls maintains or establishes a male dromedary's access to a herd of females and ensures opportunities for mating. In a close match, the bull that weathers the contests better will be the eventual winner. By starting the day cool, a bull will enhance his capacity to store heat generated by the strenuous activity, thus prolonging the onset of heat stress. A bull

that can sustain a contest for longer is more likely to win it.

Accordingly, we speculate that by lowering their daily minimum T_b during rut, bulls increase their chance of winning a harem. That is, the daily hypothermias we observed could have a direct bearing on reproductive success.

Our reasoning carries the implication that the lowering of T_b in the mornings is large enough to make a difference, and it seems that it is. Calculations show that lowering T_b by even as little as 0.6°C can make enough difference to be useful. The heat stored by a 750 kg bull for each degree of temperature rise is approximately $3.9 \text{ kJ} \cdot (\text{kg } ^\circ\text{C})^{-1} \times 750 = 2925 \text{ kJ}$ (from Withers 1992). The metabolic rate of a resting camel with a T_b of 38°C is approximately $1.2 \text{ l O}_2 \text{ min}^{-1}$ (Schmidt-Nielsen *et al.* 1967), approximately 400 W. If average metabolic rate trebles during rut contests, the additional hourly heat production would be about 2880 kJ, similar to the amount of heat stored for every degree of temperature rise. That is, lowering T_b by 1°C could allow an extra hour's activity before heat stress sets in. Even a drop of 0.6°C is likely to be of significant advantage and many drops were more than that, perhaps at times of peak rut intensity.

In summary, we report daily hypothermia in bull camels during rut and we speculate that this increases their reproductive fitness. The term adaptive heterothermy is usually applied only to the capacity of some endotherms to save water by storing heat instead of employing evaporative cooling (e.g. Mitchell *et al.* 2002). However, this seems unnecessarily restrictive; torpor and hibernation, after all, are also adaptive heterothermies. The pattern we describe in camels appears to provide yet another example.

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