biology letters

rsbl.royalsocietypublishing.org

Research

CrossMark click for updates

Cite this article: Hetem RS, Mitchell D, de Witt BA, Fick LG, Meyer LCR, Maloney SK, Fuller A. 2013 Cheetah do not abandon hunts because they overheat. Biol Lett 9: 20130472. http://dx.doi.org/10.1098/rsbl.2013.0472

Received: 22 May 2013
Accepted: 4 July 2013

Subject Areas:
behaviour, ecology

Keywords:
hyperthermia, thermal limit, exercise, sprint

Author for correspondence:
Robyn S. Hetem
e-mail: robyn.hetem@wits.ac.za

†Present address: Department of Paraclinical Science, Faculty of Veterinary Science, University of Pretoria, Onderstepoort, Pretoria, South Africa.

Electronic supplementary material is available at http://dx.doi.org/10.1098/rsbl.2013.0472 or via http://rsbl.royalsocietypublishing.org.

Royal Society Publishing
Informing the science of the future

Physiology

Cheetah do not abandon hunts because they overheat

Robyn S. Hetem[1], Duncan Mitchell[1], Brenda A. de Witt[1], Linda G. Fick[1], Leith C. R. Meyer[1,†], Shane K. Maloney[1,2] and Andrea Fuller[1]

[1]Brain Function Research Group, School of Physiology, Faculty of Health Sciences, University of the Witwatersrand Medical School, 7 York Road, Parktown 2193, South Africa
[2]School of Anatomy, Physiology and Human Biology, University of Western Australia, Stirling Highway, Crawley 6009, Australia

Hunting cheetah reportedly store metabolic heat during the chase and abandon chases because they overheat. Using biologging to remotely measure the body temperature (every minute) and locomotor activity (every 5 min) of four free-living cheetah, hunting spontaneously, we found that cheetah abandoned hunts, but not because they overheated. Body temperature averaged 38.4°C when the chase was terminated. Storage of metabolic heat did not compromise hunts. The increase in body temperature following a successful hunt was double that of an unsuccessful hunt (1.3°C ± 0.2°C versus 0.5°C ± 0.1°C), even though the level of activity during the hunts was similar. We propose that the increase in body temperature following a successful hunt is a stress hyperthermia, rather than an exercise-induced hyperthermia.

1. Introduction

Cheetah use 'stalk and chase' hunting. Although they can sprint faster than any of their potential prey [1], they are inefficient hunters, with less than 40% of hunts ending in kills [2–4]. Cheetah appear to abandon most of their chases, even when prey ought to be in range. Both successful and unsuccessful hunts are followed by long periods of inactivity, including a delay before eating after a successful hunt [5]. Their hunting inefficiency has been attributed to cheetah abandoning hunts because they overheat [6,7]. That explanation can be traced to a single study, in which Taylor & Rowntree exercised two hand-reared cheetah on a treadmill, measured heat balance and concluded that running cheetah stored metabolic heat, with the result that further exercise soon became impossible thermally, at a ceiling rectal temperature of 40.5°C [8]. Groundbreaking though the study was, it did not accurately simulate a hunt. The cheetah ran on a treadmill at maximum speeds of 30 km h^{-1} and stopped running within about 2 km. In actual hunts, cheetah can sprint at more than 100 km h^{-1} [1] and may traverse as much as 500 m [9], but typically less than 300 m [3,5]. To test whether free-living cheetah abandon hunts because they overheat, we measured the body temperature and locomotor activity of four free-living cheetah hunting naturally.

2. Material and methods

The study took place during summer, within the Tusk Trust Cheetah Rehabilitation Camp (4000 ha) of the AfriCat Foundation (20°50′ S 16°38′ E), in central Namibia. Two female and four male cheetah (*Acinonyx jubatus*), previously habituated to human presence, were allocated to the study. Body mass at surgery was 43 ± 6 kg (mean ± s.d.). We collected weather data at the field site (Hobo Weather Station, Onset Computer Corporation, USA; see the electronic supplementary material for details).

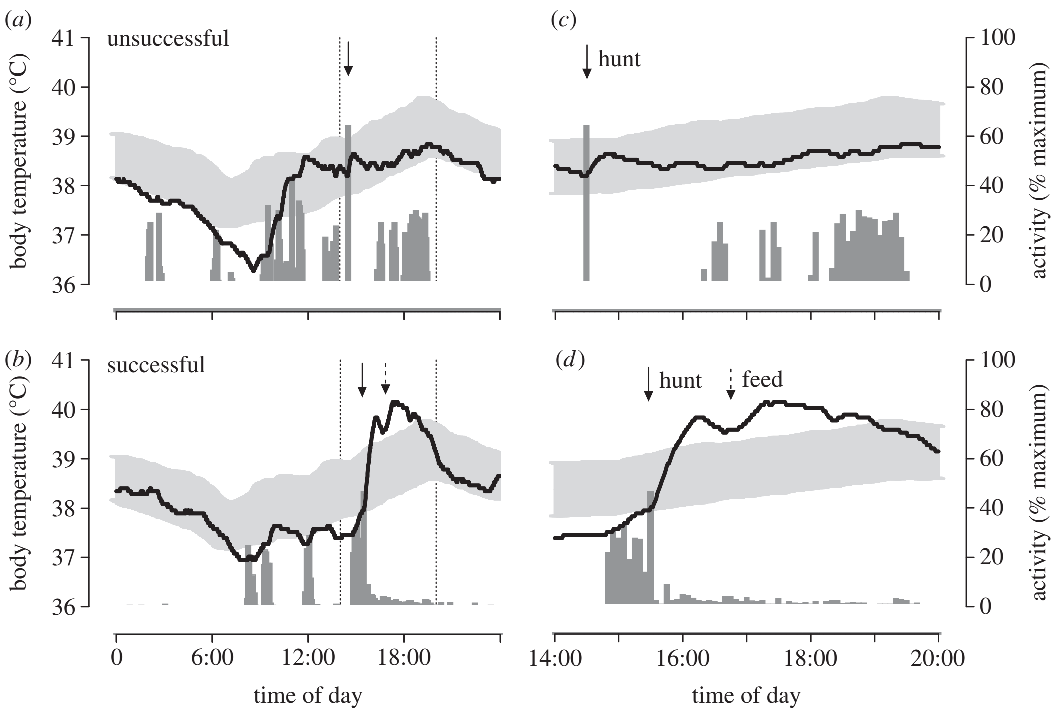

Figure 1. Body temperature (solid black line) and activity (grey vertical bars) patterns for two days during which a male cheetah (M1) was observed hunting (solid arrows). Grey bands indicate the nychthemeral body temperature rhythm (mean ± s.d.) for that cheetah. (*c*,*d*) Expansion of the areas between the dotted lines in (*a*) and (*b*), respectively. (*a*) Unsuccessful hunt on an adult female kudu (*Tragelaphus strepsiceros*). (*b*) Successful hunt on an adult warthog (*Phacochoerus aethiopicus*). Following both chases, the cheetah appeared exhausted (respiratory rate approx. 100 breaths min^{-1}) and rested in the shade for 2 h. In neither case did body temperature rise measurably during the hunt.

We implanted temperature-sensitive and movement-sensitive data loggers under sterile surgical conditions. The temperature logger (mlog_T1A, Sigma Delta Technologies, Australia, resolution 0.06°C, calibrated accuracy better than 0.1°C, approx. 25 × 25 × 10 mm, mass of approx. 10 g when covered in wax), which recorded temperature every minute, was tethered in the abdominal cavity via an incision in the *linea alba*. Another incision was made on the upper hind limb, where an activity logger was tethered subcutaneously. The activity logger (Actical, Mini-Mitter Corporation, USA, approx. 40 × 40 × 15 mm, mass of approx. 40 g when covered in wax) recorded activity over successive 5 min intervals. To compensate for inherent differences in sensitivity between individual loggers, activity was expressed as a percentage of the maximum recorded for that logger. A neck collar (African Wildlife Tracking, South Africa) carried a tracking radio transmitter on each cheetah. We measured temperature and activity for seven months during which cheetah were free to conduct their own lifestyle, including hunting naturally. We analysed body temperature and activity for 12 ± 3 (mean ± s.d.) successful and 6 ± 2 unsuccessful hunts per cheetah for four cheetah (two of the six cheetah were killed by a resident leopard). We identified successful hunts mostly by finding cheetah on fresh kills ($n = 35$) but also directly observed five successful hunts and 23 unsuccessful hunts. We used a series of generalized linear mixed models to investigate the effect of hunting on cheetah body temperature (see the electronic supplementary material).

3. Results

During the study, cheetah regulated their body temperatures around a mean of 38.3 ± 0.2°C, with a daily minimum of 37.3 ± 0.2°C and a daily maximum of 39.5 ± 0.2°C, resulting in a daily amplitude of body temperature rhythm of 2.3 ± 0.1°C (see the electronic supplementary material). Body temperature seldom exceeded the 40.5°C ceiling [8], and far less often than the cheetah abandoned hunts. Body temperature profiles differed between successful and unsuccessful hunts (figure 1). Hunts were associated with a transient increase in activity, often confined to one 5-min interval of the logger, usually preceded by a more extended period of lower-level activity; these two kinds of activity reflected the searching and stalking of prey and then the chase. Successful and unsuccessful hunts were both followed by long periods of inactivity or low activity; the cheetah in figure 1 was inactive for nearly 2 h after that unsuccessful hunt. Body temperature did not rise significantly during the chase. Cheetahs' body temperature at the time chases were terminated did not differ from their mean 24-h body temperature, for either successful (38.4 ± 0.2°C, $t_3 = 0.68$, $p = 0.55$) or unsuccessful (38.3 ± 0.2°C, $t_3 = 0.24$, $p = 0.82$) chases. The main factor affecting body temperature when the chase was terminated was the time of day when the hunt occurred and, by implication, the body temperature of the cheetah when the hunt started, as determined by the 24-h rhythm of body temperature (table 1).

(a) Comparison between successful and unsuccessful hunts

Although body temperature did not increase significantly during the chase, hunting did have thermal consequences. The temperature profile of cheetah for all hunts was similar to those shown in figure 1. Following successful hunts, body temperature increased steadily for an average of 40 min and by 1.3 ± 0.2°C, while after unsuccessful hunts it increased by only 0.5 ± 0.1°C. We investigated whether success of the hunt (i.e. successful or unsuccessful) affected the cheetah's body temperature profile, controlling statistically for the effects of maximum hunt activity, duration of the hunt, time of day when the hunt occurred and

Table 1. Generalized linear mixed model results for the relationship between parameters of the body temperature profiles of hunting cheetah and hunt attributes. Note: cheetah identity was included as a random factor. $n = 63$ hunts. Italicized values indicate $p < 0.05$.

	$\beta \pm$ s.e.	Z	p	95% CI
body temperature at time of maximum activity (°C)				
success of the hunt	−0.0929 ± 0.1376	−0.68	0.50	−0.3626 to 0.1768
maximum activity during the hunt	0.0019 ± 0.0023	0.82	0.42	−0.0026 to 0.0064
duration of the hunt	0.0033 ± 0.0017	1.94	0.05	−0.0000 to 0.0067
time of day when hunt occurred	0.0840 ± 0.0203	4.14	*0.000*	0.0443 to 0.1238
air temperature when hunt occurred	−0.0273 ± 0.0126	−2.16	*0.03*	−0.0521 to −0.0026
maximum body temperature reached (°C)				
success of the hunt	−0.8355 ± 0.1445	−5.77	*0.000*	−1.1194 to −0.5515
maximum activity during the hunt	0.0020 ± 0.0025	0.82	0.42	−0.0028 to 0.0069
duration of the hunt	0.0019 ± 0.0018	1.01	0.31	−0.0017 to 0.0055
time of day when hunt occurred	0.1099 ± 0.0217	5.07	*0.000*	0.0674 to 0.1524
air temperature when hunt occurred	−0.0089 ± 0.0134	−0.67	0.51	−0.0351 to 0.0173
body temperature increase (°C)				
success of the hunt	−26.5421 ± 6.9112	−3.84	*0.000*	−40.0879 to −12.996
maximum activity during the hunt	−0.1918 ± 0.1154	−1.66	0.10	−0.4180 to 0.0343
duration of the hunt	−0.1010 ± 0.0866	−1.17	0.24	−0.2708 to 0.0688
time of day when hunt occurred	0.5148 ± 1.0295	0.5	0.62	−1.5030 to 2.5326
air temperature when hunt occurred	−0.3758 ± 0.6579	−0.57	0.57	−1.6653 to 0.9136
area under the temperature increase/time curve (°C min)				
success of the hunt	−65.3126 ± 14.017	−4.66	*0.000*	−92.7861 to −37.8392
maximum activity during the hunt	0.0713 ± 0.2378	0.30	0.76	−0.3948 to 0.5375
duration of the hunt	0.4607 ± 0.1782	2.58	*0.010*	0.1114 to 0.8101
time of day when hunt occurred	2.2280 ± 2.1053	1.06	0.29	−1.8985 to 6.3544
air temperature when hunt occurred	0.0850 ± 1.3149	0.06	0.95	−2.4922 to 2.6623

air temperature (table 1). Compared to unsuccessful hunts, successful hunts were associated with significantly higher subsequent peak body temperature (39.2 ± 0.2°C versus 38.7 ± 0.2°C, $p < 0.001$), body temperature increase (1.3 ± 0.2°C versus 0.5 ± 0.1°C, $p < 0.001$) and area under the temperature/time curve (78 ± 19°C min^{-1} versus 8 ± 9°C min^{-1}, $p < 0.001$).

(b) Factors that increase body temperature following successful hunts

Having established that successful hunts differed thermally from unsuccessful hunts, we investigated the effect that various hunt-related factors had on the cheetah's body temperature profile following successful hunts (table 2). Time of day at which the hunt occurred was the only factor that significantly influenced the maximum body temperature following successful hunts ($p = 0.01$); maximum activity of the hunt, duration of the hunt, air temperature and prey mass had no significant effect on the maximum body temperature after a hunt. Although they did not affect the maximum body temperature, both duration of the hunt and maximum activity of the hunt significantly affected the rate of increase in body temperature. Duration of the hunt significantly affected the integrated temperature increase over time (area under curve; $p = 0.01$). Air temperature at the time of the hunt, and body mass of the prey, did not significantly influence the cheetah's body temperature profile following successful hunts (table 2).

4. Discussion

Using biologging to measure activity and body temperature in free-living cheetah hunting spontaneously in their natural habitat, we have shown that our cheetah abandoned hunts, but not because they overheated. Even when one male cheetah (M1) came close to the maximum chase distance (300 m) reported for cheetah [3], its temperature did not increase measurably during the chase (figure 1*a*). At the termination of intense activity during hunts, body temperatures did not exceed those of the 24-h rhythm and did not reach the 40.5°C thermal limit to exercise reported for cheetah running on a treadmill [8]. Indeed, body temperature reached 40.5°C so seldom that the supposed thermal limit to exercise of 40.5°C appeared irrelevant in these free-living cheetah. Following the termination of unsuccessful hunts, body temperatures increased at approximately 0.03°C min^{-1} over 15 min, only a fraction of the rate (1.6°C min^{-1}) predicted if cheetah stored 90% of the heat produced during a 110 km h^{-1} sprint [8]. The absence of a measurable increase in body temperature during chases was not the result of thermal inertia of the logger ($\tau = 3$ min). Metabolic heat during

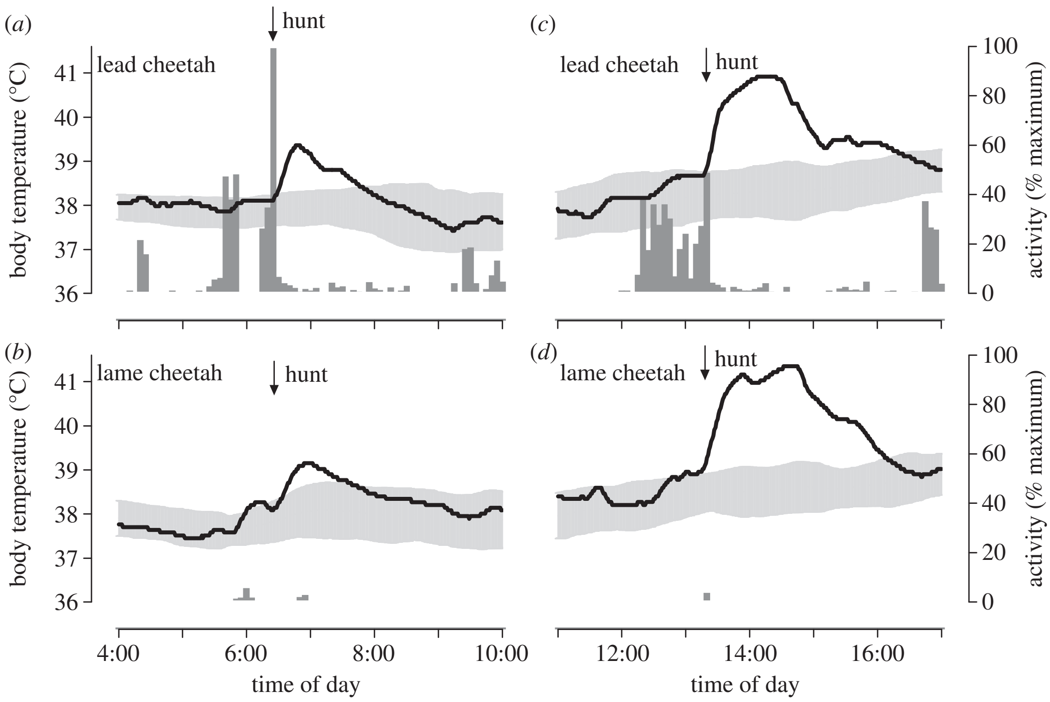

Figure 2. Body temperature (solid black line) and activity (grey vertical bars) pattern for two cheetah siblings. Grey bands indicate the nychthemeral body temperature rhythm (mean ± s.d.) for each cheetah. (*a*) The female cheetah (F2) hunted a steenbok (*Raphicerus campestris*) at 06:30 (arrow). (*b*) The male cheetah (M3) joined his sibling shortly after the hunt; he had a thorn in his foot, was unable to run, and had not participated in the hunt. Note, however, the similar increase in body temperature after the hunt. The female cheetah presumably hunted again the next day (*c*,*d*), although the hunt was not confirmed by visual observation.

Table 2. Generalized linear mixed model results for the relationship between parameters of the body temperature profiles of cheetah after successful hunts, and hunt attributes. Cheetah identity was included as a random factor. $n = 40$ successful hunts. Italicized values indicate $p < 0.05$.

	$\beta \pm$ s.e.	Z	p	95% CI
maximum body temperature reached (°C)				
maximum activity during the hunt	0.0024 ± 0.0038	0.64	0.52	−0.0050 to 0.0098
duration of the hunt	0.0021 ± 0.0021	0.94	0.35	−0.0022 to 0.0064
time of day when hunt occurred	0.0923 ± 0.0332	2.78	*0.005*	0.0272 to 0.1574
air temperature when hunt occurred	−0.0037 ± 0.0203	−0.18	0.86	−0.0435 to 0.0362
prey mass	−0.0029 ± 0.0027	−1.07	0.28	−0.0082 to 0.0024
body temperature increase (°C)				
maximum activity during the hunt	−0.0004 ± 0.0036	−0.11	0.91	−0.0074 to 0.0066
duration of the hunt	0.0041 ± 0.0021	1.96	0.05	0.0000 to 0.0081
time of day when hunt occurred	0.0242 ± 0.0314	0.77	0.44	−0.0374 to 0.0858
air temperature when hunt occurred	−0.0076 ± 0.0192	−0.39	0.69	−0.0453 to 0.0301
prey mass	−0.0031 ± 0.0026	−1.20	0.23	−0.0081 to 0.0019
rate of body temperature change (°C min^{-1})				
maximum activity during the hunt	0.0002 ± 0.0000	2.79	*0.005*	0.0000 to 0.0004
duration of the hunt	−0.0001 ± 0.0000	−2.91	*0.004*	−0.0002 to 0.0000
time of day when hunt occurred	0.0012 ± 0.0007	1.56	0.12	−0.0003 to 0.0026
air temperature when hunt occurred	0.0001 ± 0.0005	0.27	0.79	−0.0008 to 0.0010
prey mass	−0.0000 ± 0.0000	−0.50	0.62	−0.0002 to 0.0000
area under the temperature increase/time curve (°C min)				
maximum activity during the hunt	0.0240 ± 0.3809	0.06	0.95	−0.7226 to 0.7706
duration of the hunt	0.5755 ± 0.2237	2.57	*0.01*	0.1371 to 1.0139
time of day when hunt occurred	3.7064 ± 3.3926	1.09	0.28	−2.9430 to 10.3557
air temperature when hunt occurred	−0.7017 ± 2.1163	−0.33	0.74	−4.8496 to 3.4462
prey mass	−0.3513 ± 0.2783	−1.26	0.21	−0.8967 to 0.1942

chases would have been generated mainly in leg muscles, but we expect redistribution from highly perfused muscles in minutes, with delay unrelated to hunt success.

After successful hunts, cheetah rested at their prey and did not immediately begin eating but body temperature increased. Therefore, the larger increase in body temperature after a successful than an unsuccessful hunt could not be attributed to heat increments of feeding. Body temperatures sometimes remained elevated above normal for the 24-h rhythm for more than an hour after the hunt (figure 1*b*). The elevation was not related to activity levels, air temperature or heat released during the subduing of prey. Cheetah suffocate their prey at the neck and strangulation may take up to 10 min [5], but the cheetah's nasal anatomy allows effective evaporative cooling during the act [10], provided the vapour pressure of the air is sufficiently low. If the 1.3°C rise in body temperature following successful hunts resulted from metabolic heat generated during the chase, metabolic rate during the chase would have had to be equivalent to about 1200 ml kg^{-1} min^{-1} of oxygen consumption (170 times the resting metabolic rate of cheetah), an unattainable power even from combined aerobic and anaerobic sources. We propose that the increased body temperature that followed successful hunts was a stress hyperthermia, a phenomenon associated with high sympathetic nervous system activity, similar to the fear-induced hyperthermia exhibited by antelope [11]. Figure 2 shows evidence supporting that hypothesis: the post-hunt hyperthermia was similar in two cheetah, one of which had chased and killed the prey, whereas the other was lame, unable to hunt and simply shared the prey. Cheetah have been described as 'nervous at kills' [5] and 'alert when feeding' [12]. Cheetah frequently stop feeding to survey the surrounding area [12], perhaps demonstrating vigilance for more dominant predators such as lion and leopard [13,14]. Two of our cheetah were killed by a resident leopard during our study.

Body temperature data from our free-living cheetah hunting spontaneously, by ambush in a densely vegetated area, do not support the dogma that cheetah abandon hunts because they overheat. Our cheetah abandoned chases for other, yet unknown, reasons. Whether hunts induce a higher core temperature in cheetah using open-pursuit hunting patterns in grasslands, or in cheetah exposed to hotter environments, remains to be investigated.

Procedures were approved by the Animal Ethics Screening Committee of the University of the Witwatersrand (protocol no. 2005/42/4).

Acknowledgements. We thank the AfriCat Foundation, the Hanssen family and the guides at Okonjima for supporting the research. We particularly thank C. Conradie and D. Houghtan for their hospitality and M. Jago for veterinary assistance. We thank R. McFarland for assistance with generalized linear mixed models.

Funding statement. This research was supported by the National Research Foundation of South Africa and a Carnegie Large Research grant.

References

1. Sharp NCC. 1997 Timed running speed of a cheetah (*Acinonyx jubatus*). *J. Zool. Lond.* **241**, 493–494. (doi:10.1111/j.1469-7998.1997.tb04840.x)
2. Eaton RL. 1970 Hunting behavior of the cheetah. *J. Wildl. Manage.* **34**, 56–67. (doi:10.2307/3799492)
3. Mills MGL, Broomhall LS, du Toit JT. 2004 Cheetah *Acinonyx jubatus* feeding ecology in the Kruger National Park and a comparison across African savanna habitats: is the cheetah only a successful hunter on open grassland plains? *Wildl. Biol.* **10**, 177–186.
4. Hilborn A, Pettorelli N, Orme CDL, Durant SM. 2012 Stalk and chase: how hunt stages affect hunting success in Serengeti cheetah. *Anim. Behav.* **84**, 701–706. (doi:10.1016/j.anbehav.2012.06.027)
5. Schaller GB. 1968 Hunting behaviour of the cheetah in the Serengeti National Park, Tanzania. *E. Afr. Wildl. J.* **6**, 95–100. (doi:10.1111/j.1365-2028.1968.tb00906.x)
6. Bartholomew GA. 1982 Body temperature and energy metabolism. In *Animal physiology: principles and adaptations* (eds MS Gordon, GA Bartholomew, AD Grinnel, CB Jørgensen, FN White), pp. 333–406, 4th edn. New York, NY: MacMillan Publishing Co.
7. Vaughan TA, Ryan JM, Czaplewski NJ. 2011 *Mammalogy*, 5th edn. Sudbury, Canada: Jones and Bartlett Publishers.
8. Taylor CR, Rowntree VJ. 1973 Temperature regulation and heat balance in running cheetahs: a strategy for sprinters? *Am. J. Physiol.* **224**, 848–851.
9. Hunter L, Hamman D. 2003 *Cheetah*, pp. 88–116. Cape Town, South Africa: Struik Publishers.
10. Torregrosa V, Petrucci M, Pérez-Claros JA, Palmqvist P. 2010 Nasal aperture area and body mass in felids: ecophysiological implications and paleobiological inferences. *Geobios* **43**, 653–661. (doi:10.1016/j.geobios.2010.05.001)
11. Meyer LCR, Fick LG, Matthee A, Mitchell D, Fuller A. 2008 Hyperthermia in captured impala (*Aepyceros melampus*): a fright not flight response. *J. Wildl. Dis.* **44**, 404–416.
12. Phillips JA. 1993 Bone consumption by cheetahs at undisturbed kills: evidence for a lack of focal-palatine erosion. *J. Mammal.* **74**, 487–492. (doi:10.2307/1382408)
13. Hunter JS, Durant SM, Caro TM. 2007 To flee or not to flee: predator avoidance by cheetahs at kills. *Behav. Ecol. Sociobiol.* **61**, 1033–1042. (doi:10.1007/s00265-006-0336-4)
14. Durant SM. 2000 Predator avoidance, breeding experience and reproductive success in endangered cheetahs, *Acinonyx jubatus*. *Anim. Behav.* **60**, 121–130. (doi:10.1006/anbe.2000.1433)