

Body temperature, activity patterns and hunting in free-living cheetah: biologging reveals new insights

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Abstract

As one of the few felids that is predominantly diurnal, cheetahs (*Acinonyx jubatus*) can be exposed to high heat loads in their natural habitat. Little is known about long-term patterns of body temperature and activity (including hunting) in cheetahs because long-term concurrent measurements of body temperature and activity have never been reported for cheetahs, or, indeed, for any free-living felid. We report here body temperature and locomotor activity measured with implanted data loggers over 7 months in 5 free-living cheetahs in Namibia. Air temperature ranged from a maximum of 39 °C in summer to -2 °C in winter. Cheetahs had higher (~0.4 °C) maximum 24-h body temperatures, later acrophase (~1 h), with larger fluctuations in the range of the 24-h body temperature rhythm (approximately 0.4 °C) during a hot-dry period than during a cool-dry period, but maintained homeothermy irrespective of the climatic conditions. As ambient temperatures increased, the cheetahs shifted from a diurnal to a crepuscular activity pattern, with reduced activity between 900 and 1500 hours and increased nocturnal activity. The timing of hunts followed the general pattern of activity; the cheetahs hunted when they were on the move. Cheetahs hunted if an opportunity presented itself; on occasion they hunted in the midday heat or in total darkness (new moon). Biologging revealed insights into cheetah biology that are not accessible by traditional observer-based techniques.

Key words: *Acinonyx jubatus*, heat stress, nocturnal, intraguild predators, moonlight

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Introduction

Historically, cheetahs [*Acinonyx jubatus* (Schreber, 1775)] have been classified as diurnally active hunters (Estes 1991; Skinner & Chimimba 2005). Diurnal hunting may reduce the risk of encountering larger, more dominant predators, which are primarily nocturnal (Hayward & Slotow 2009). The idea that cheetahs are diurnal hunters stems from traditional observations of

behavior, which are accomplished more easily in daylight. The advent of biologging technology to record activity remotely and continuously has already dispelled the proposition that cheetahs are strictly diurnal. Biologging has revealed a surprisingly high level of nocturnal activity among cheetahs (Hayward & Slotow 2009; Cozzi *et al.* 2012; Broekhuis *et al.* 2014). What is not yet known is why cheetahs are sometimes nocturnally active despite the threat from more dominant predators. One possibility is the avoidance of diurnal heat stress; cheetahs are less active overall when ambient temperatures are high (Cozzi *et al.* 2012).

To explore thermoregulation in cheetahs, we have used biologging to record body core temperatures of free-living cheetahs. Continuous measurement of the body temperature rhythms of captive cheetahs in a zoo, by biotelemetry in the early days of its application (Asa & Sarrik 1990), had led to the conclusion that cheetahs and other large felids may not have a circadian rhythm of body temperature, or of activity (Bircher & Noble 1997). Free-living cheetah, however, exhibited a well-controlled nycthemeral (i.e. associated with the 24-h cycle, with exogenous cues like light) rhythm of body temperature (as shown in Fuller *et al.* 2016) interspersed by sporadic hyperthermias. Those sporadic hyperthermias were not a result of ambient heat stress but occurred after successful hunts. We proposed (Hetem *et al.* 2013) that they were sympathetically-mediated stress hyperthermias, related to the cheetah being most vulnerable to more dominant intraguild predators while guarding their prey.

Biologging technology, therefore, has already revealed new insights into the biology of cheetahs, but there remain other questions that the technology could address. For example, it could be used to measure when hunts occur and whether those hunts were successful, because we have identified the profiles of body temperature that are unique to successful hunts (Hetem *et al.* 2013). Potentially, a more important contribution of biologging technology could be the measurement of how various functions interact in free-living cheetahs. We hypothesized that cheetahs would display seasonal variation in their body temperature and activity patterns. Because high levels of activity, presumably hunts, may increase body temperature, we hypothesized that cheetahs may shift to a nocturnal activity pattern to avoid hyperthermia during hot periods, without compromising total 24-h activity. In addition, because hunger does not appear to be the trigger for cheetah hunts (Cooper *et al.* 2007), we hypothesized that hunts occur when cheetahs

are otherwise active. Ongoing locomotor activity could affect a cheetah's readiness for the intense activity of a chase (Wilson *et al.* 2013). Using data gathered by implanted biologgers from 5 cheetahs over 7 months (i.e. the same dataset used previously to detect thermal implications of hunts; Hetem *et al.* 2013), we set out to address the links between hunting, other locomotor activity, body temperature and the thermal environment, in free-living cheetahs behaving naturally, and in their traditional habitat. Unintentionally, we also recorded on our biologgers the consequences of encounters between our cheetahs and leopards, *Panthera pardus* Linnaeus, 1758, one of those more dominant predators that cheetahs could be seeking to avoid by being active diurnally.

Materials and Methods

Study area

The study took place between September and May (austral summer) within the TUSK Trust Cheetah Rehabilitation Camp (4000 ha surrounded by a predator-proof fence, impassable to cheetahs) of the AfriCat Foundation, on the farm Okonjima (20°50'S 16°38'E) in central Namibia, in the historical and current distribution range of cheetahs (Durant *et al.* 2017). Okonjima lies in a summer rainfall region and is predominantly shrubland and thornbush savanna. Potential prey species for cheetahs that were common in the camp included warthog [*Phacochoerus africanus* (Gmelin, 1788)] and several antelope species (including kudu [*Tragelaphus strepsiceros* (Pallas, 1766)], blue wildebeest [*Connochaetes taurinus* (Burchell, 1823)], gemsbok [*Oryx gazella* (Linnaeus, 1758)], red hartebeest [*Alcelaphus caama* (É. Geoffroy Saint-Hilaire, 1803)], impala [*Aepyceros melampus* (Lichtenstein, 1812)], steenbok [*Raphicerus campestris* (Thunberg, 1811)], common duiker [*Sylvicapra grimmia* (Linnaeus, 1758)] and Damara dik-dik [*Madoqua kirkii* (Günther, 1880)]), zebra (*Equus quagga* Boddaert, 1785 and *Equus hartmannae* Matschie, 1898), various smaller mammal species and birds. Two resident leopards with their cubs constituted intraguild predators.

Study animals

Procedures were approved by the Animal Ethics Screening Committee of the University of the Witwatersrand (protocol no. 2005/42/4). We used 2 female and 4 male adult cheetahs that were habituated to human presence as part of a rehabilitation program and were due to be released from captivity into the wild. Two of the male cheetahs (males 1 and 2) had previous hunting

experience in the wild. Four siblings (males 3 and 4 and females 1 and 2) had been raised in captivity after being orphaned at 6 months of age, and remained together as a coalition after being released into the wild. However, the females were observed hunting independently on occasion. Male 4 was euthanized 2 months after release into the wild, following a leopard attack that severed his spine; his data, therefore, were excluded from the main analyses. At the start of the study, the 5 cheetahs that were subsequently included in the analyses had a body mass of 43 ± 6 kg (mean \pm SD, range 38–52 kg).

Temperature and activity measurements

We implanted 2 miniature temperature-sensitive data loggers intra-abdominally. One data logger (StowAway XTI, Onset Computer Corporation, Pocasset, MA, USA) recorded temperature at 10-min intervals, had a resolution of 0.04 °C and measurement range from 34 to 46 °C. The second data logger (mlog_T1A, Sigma Delta Technologies, Perth, Australia) recorded temperatures every minute and had a resolution of 0.06 °C. Each pair of data loggers was assembled as a single unit, covered in an inert wax (Sasol EXP986, Johannesburg, South Africa) and dry-sterilized in formaldehyde vapor before implantation. The logger package had dimensions of approximately 70 × 60 × 20 mm and a mass of approximately 50 g when coated in wax. The data loggers were calibrated individually, in an insulated water bath, against a high-accuracy thermometer (Quat 100, Heraeus, Hanau, Germany). Calibrated accuracy was better than 0.1 °C.

The activity loggers (Actical, Mini-Mitter Corporation, Bend, USA) recorded movement over successive 5-min epochs, using a multidirectional, piezoelectric accelerometer, which was sensitive to 0.05 g. These loggers had dimensions of 40 × 40 × 15 mm, and weighed approximately 40 g when covered in the same wax. The activity loggers were orientated so that the axis with highest sensitivity (designated by the manufacturer) was parallel to the long axis of the body (i.e. the primary direction of locomotor movement). To account for differences in the sensitivity of individual activity loggers, we expressed activity as a percentage of the maximum reading that each logger recorded at any time after implantation, a normalization procedure that we have used previously (e.g. Hetem *et al.* 2008).

Surgical procedure

The cheetahs were darted and anesthetized in their holding pens with medetomidine hydrochloride (0.023

± 0.002 mg·kg⁻¹; Domitor, Novartis, Kempton Park, South Africa) and a tiletamine hydrochloride and zolazepam hydrochloride combination (1.5 ± 0.2 mg·kg⁻¹; Zoletil, Virbac Animal Health, Midrand, South Africa) and, once recumbent, were transported to a nearby operating theatre. They were intubated and anesthesia was maintained with 2–4% halothane (Fluothane, Astra Zeneca, Johannesburg, South Africa), administered in 100% oxygen. Vital signs were monitored throughout the surgical procedure, which lasted approximately 55 min per cheetah.

We shaved and sterilized incision sites with chlorhexidine gluconate (Hibitane, Zeneca, Johannesburg, South Africa). A 50-mm cranial–caudal incision was made through the skin and *linea alba* and 2 miniature temperature-sensitive data loggers were inserted intra-abdominally as a single unit and tethered to the ventral abdominal wall. A second incision was made on the upper hind limb at a site locally anesthetized (0.04 g lignocaine hydrochloride s.c.; Bayer Animal Health, Isando, South Africa), where an activity-sensitive data logger (see description below) was tethered subcutaneously. The muscle and skin layers were sutured closed. Wounds were sprayed with a topical antiseptic spray (Necrospray, Centaur Labs, Johannesburg, South Africa) and coated with a topical ectoparasiticide (tick grease, cypermethrin 0.025% m/m; Bayer Animal Health, Isando, South Africa). Each cheetah received a penicillin-based antibiotic (5-mL procaine benzylpenicillin 150 mg·ml⁻¹ and benzathine benzylpenicillin 126 mg·ml⁻¹ i.m.; Peni LA Phenix, Virbac Animal Health, Centurion, South Africa), an analgesic (0.02 mg·kg⁻¹ buprenorphine s.c.; Temgesic, Kyron Laboratories, Johannesburg, South Africa) and a non-steroidal anti-inflammatory (1.75 mg·kg⁻¹ carprofen s.c.; Rimadyl, Pfizer, South Africa) medication.

A neck collar housing a radio-tracking transmitter (African Wildlife Tracking, Pretoria, South Africa) was fitted to each cheetah. The action of medetomidine was reversed with atipamezole hydrochloride (1.5 mg i.m.; Antisedan, Novartis, Kempton Park, South Africa) and cheetahs were placed in individual crates to recover from the anesthetic before being transported back to their pens. After a 2-week recovery period during which there were no signs of post-surgical complications, the cheetahs were released into the camp in October.

Cheetahs were monitored regularly. In addition to male 4 who had the early encounter with a leopard (see above), a second male cheetah (male 2) developed gastritis in mid-November, was removed from the camp and was treated for 2 months in captivity, during which

time his activity logger was removed. He was released again after recovery but was found dead in mid-May; bite marks along his spine led us to believe that he also was killed by a leopard. We recovered his data loggers post-mortem. Seven months after the initial release, in late May, the 4 surviving cheetahs were darted in the field with a combination of medetomidine hydrochloride ($0.025 \pm 0.003 \text{ mg}\cdot\text{kg}^{-1}$ i.m.; Domitor, Novartis) and ketamine hydrochloride ($3.0 \pm 0.3 \text{ mg}\cdot\text{kg}^{-1}$; Anaket-V, Bayer Animal Health). Their data loggers were removed during a surgical procedure similar to that used for the original implantation. After recovery from anesthesia, these cheetahs were returned to the camp, and continued to live there without apparent sequelae from the study procedures.

Climatic data measurements

We erected a portable weather station (Hobo Weather Station, Onset Computer Corporation, Pocasset, USA) in an open area and recorded dry-bulb temperature, relative humidity, wind speed, solar radiation and standard (150-mm diameter) black globe temperature, at a height of 1 m, at 30-min intervals. From the measurements of black globe temperature, air temperature and relative humidity, we calculated the wet bulb globe temperature index (Lemke & Kjellstrom 2012), an index of environmental stress that is used to assess the safety of the thermal environment for exercising humans (see for example Nassis *et al.* 2015). Rainfall was measured using a rain gauge on site. Phases of the moon and photoperiod, as well as sunrise and sunset times were obtained from the US Naval Observatory website (<http://aa.usno.navy.mil/data/>) and times of solar noon were obtained from the USNO website (<http://www.solar-noon.com/>). Phase of the moon was converted to a value between zero and one based on the fraction of the moon that was illuminated.

Data analysis

In addition to the major events described above, other incidental events led to temporary loss of data. Male 1 was injured while hunting a zebra in late November. He was darted for treatment of his wounds, at which time his activity logger had to be removed as it had broken through the skin. He remained in captivity for 10 days. He was found injured again in February and spent 19 days in captivity while undergoing treatment. Female 2 injured a foot in late December and was kept in captivity for just over 1 month. Data during periods of recovery in captivity (males 1 and 2 and female 2) were re-

moved from our analyses. The total number of days of free-living data per individual ranged between 150 and 221 days.

To help resolve whether the thermal environment affected body temperature, we divided our observation period into 3 seasonal periods based on the prevailing climatic conditions, which we called hot-dry (October–December), warm-wet (January–March) and cool-dry (April–May). We averaged each climatic variable over successive 24-h periods and compared these averages for the seasonal periods using 1-way ANOVAs. Those seasonal periods gave us 3 periods of different thermal stress on the cheetahs. We then calculated the mean of the body temperatures of each cheetah at each 10-min interval over successive 24-h periods, extracted the minimum and maximum temperatures within each 24-h period, and calculated the range of 24-h body temperature variation as the difference between the 24-h minimum and the 24-h maximum. We also recorded the time of day at which both the minimum and maximum 24-h body temperature occurred. We averaged the 24-h body temperature variables for each cheetah for all days that each cheetah was living free in the camp within each seasonal period, and then averaged those individual values over all cheetahs in the group. We also noted the absolute maximum body temperature reached by each cheetah within each seasonal period. We performed repeated-measures ANOVAs to test for differences in the 24-h body temperature profile across the 3 seasonal periods. Tukey's multiple comparison tests were used to identify sources of significant differences in ANOVAs.

Because hunts, and perhaps other activities, resulted in large and irregular fluctuations in body temperature (see Hetem *et al.* 2013), we used cosinor analysis (Nelson *et al.* 1979) to identify the parameters of the underlying rhythm of body temperature without undue influence from those irregular fluctuations. We fitted cosinor curves to the raw (10-min) body temperature data of each cheetah, for each 24-h period, and averaged the 10-min body temperature, mesor, minimum, maximum, amplitude and acrophase of the fitted curves for each cheetah for each of the 3 seasonal periods. Because we fitted a symmetric cosinor curve, the nadir would occur 12 h prior to the acrophase and was, therefore, excluded from analyses. We then averaged individual values over all cheetahs in the group. These variables were compared across the 3 seasonal periods by means of repeated-measures ANOVAs, with Tukey's multiple comparison tests used to identify sources of significant differences.

To further explore the relationship between environmental conditions and body temperature patterns, as well as a possible relationship between ongoing activity and body temperature profiles, we used a series of generalized linear mixed-effects models with Gaussian error and identity link (hereafter GLMMs) to investigate the association between various environmental and activity variables (total or maximum 24-h activity) and the cheetahs' body temperature profile. The data that we used in the analysis were the values of the environmental variables and the total or maximum 24-h activity for each cheetah, for each 24-h period, over the entire study period, that is a total of 954 cheetah-days. We entered the mass and sex of each individual cheetah as "control variables" because of their potential impact on that profile. In all GLMMs we entered days since winter solstice nested within individual cheetahs as random factors to control for the non-independence of data points, allowing each day to be entered as a single data point (Pinheiro & Bates 2000).

To explore possible patterns of activity in our free-living cheetahs, we averaged the activity within each 5-min epoch of the day for each cheetah, over all the days for which we had activity records for that cheetah in each seasonal period. We also calculated, for each cheetah on each day, the total activity for the 24 h, the maximum activity in any 5-min epoch in each 24-h period, the time of maximum activity, the proportion of that activity that occurred at night (between sunset and sunrise), and the proportion of the activity that occurred during the heat of the day (between 9:00 and 15:00 hours), and averaged those values for each seasonal period. We averaged those individual values over all cheetahs in the group, for each of the 3 seasonal periods.

To explore the relationship between environmental conditions and activity patterns, we used GLMMs. Again, the data that we used in the analysis were the values, for each 24-h period, for the environmental variables and the daily activity data for each cheetah, over the entire study period; that is, a total of 571 cheetah-days. We entered the mass and sex of individual cheetah as "control variables," and days since winter solstice nested within individual cheetahs as random factors.

To investigate hunting behavior, we used the activity and body temperature profiles that we had established previously to characterize hunts in the same cheetahs (Hetem *et al.* 2013) to identify putative chases. We assumed that activity within a 5-min epoch greater than 60% of the maximum activity recorded by each logger

constituted a putative chase. The chase was classified as successful if body temperature increased by more than 0.5 °C within 30 min of the spike of activity identifying the time of the chase; successful and unsuccessful hunts have different post-hunt temperature profiles (Hetem *et al.* 2013). From the model, we calculated the number of putative chases undertaken by each cheetah, the number of those that were successful, and the number that took place between sunset and sunrise (nocturnal), within each 24-h period for each cheetah. To explore the relationship between hunt variables and environmental variables and general activity, we used GLMMs to investigate the association between various hunt variables, environmental variables and activity variables. We used Poisson regressions for count data. Again, the data that we used in the analysis were the values, for each 24-h period, for the environmental variables and the hunt data for each cheetah, over the entire study period. There were a total of 571 cheetah-days in the analysis, and the model predicted that cheetahs hunted successfully on 337 of those cheetah-days. We entered the mass and sex of individual cheetah as "control variables," and days since winter solstice nested within individual cheetahs as random factors.

All GLMMs were performed in STATA v12 software (StataCorp, College Station, USA). Other statistical analyses were performed using GraphPad Prism (version 4.00 for Windows, GraphPad Software, San Diego, CA, USA). Data are expressed as mean \pm SD, and $P < 0.05$ was considered statistically significant.

Results

Climate

In addition to differing in temperature (see raw data plot in Fig. S1A) and rainfall, the 3 selected seasonal periods also differed in wind speed, solar radiation, water vapor pressure and photoperiod (Table 1). Air and black globe temperature varied as a function of time of day, peaking soon after solar noon and reaching a minimum just before sunrise (Fig. 1c). The daily maximum air temperature reached 38.8 °C in November and the daily minimum was -2.0 °C in May. There was seldom any cloud cover, except during rain storms; black globe temperature, which integrates heat load from radiation with air temperature and wind speed, reached 56 °C in November. Solar radiation showed the expected bell-shaped distribution over the day and wind speed was highest in the late afternoon. Rainfall totaled 931 mm over the study period, double the previous 5-year aver-

age of 432 ± 132 mm. Although the 2 dry periods had only 10% of the rain that fell during the wet period (Table 1), the vegetation remained dense during the cool-dry period following the high rainfall of the preceding cool-wet season.

Body temperature

The body temperature of the cheetahs usually varied between 37.2 and 39.6 °C, but there were occasions when body temperature exceeded 40 °C and also where it was lower than 36 °C (Suppl. Fig. S1b). Body temperatures were lowest shortly after sunrise, and peaked shortly before sunset (Fig. 1a). The nycthemeral rhythm of body temperature differed seasonally, as reflected in both the raw data (Fig. 1a) and the cosinor analysis (Fig. 1b). However, neither the mean nor the

mesor of the 24-h body temperature rhythm varied significantly across the seasonal periods (Table 2), and for the whole 7-month period, the mean 24-h body temperature and the mesor of the cosinor rhythm for the cheetahs was 38.3 ± 0.2 °C ($n = 5$).

Although mean 24-h body temperature did not differ between the seasonal periods (Table 2), the mean maximum 24-h body temperature was lower in the cool-dry period than in both the hot-dry ($P < 0.05$) and warm-wet ($P < 0.05$) periods. Because the minimum 24-h body temperature was not different between the periods (Table 2), the lower maximum 24-h body temperatures in the cool-dry period resulted in a smaller range of 24-h body temperature rhythm in the cool-dry period than that in the hot-dry period ($P < 0.01$). However, that smaller range (2.0 ± 0.2 °C) was only marginally

Table 1 Environmental conditions (mean \pm SD) during the 3 seasonal periods

Environmental variables	Hot-dry October–December (79 days)	Warm-wet January–March (90 days)	Cool-dry April–May (53 days)
Air temperature (°C)			
24-h mean	23.9 ± 2.1^a	20.2 ± 1.6^b	15.4 ± 2.8^c
24-h maximum	33.7 ± 2.3^a	28.2 ± 2.4^b	25.6 ± 2.4^c
24-h minimum	14.2 ± 3.7^a	14.9 ± 2.0^a	7.6 ± 4.8^b
24-h range	19.4 ± 3.9^a	13.4 ± 3.2^b	18.0 ± 4.6^a
Black globe temperature (°C)			
24-h mean	27.8 ± 2.4^a	23.6 ± 2.3^b	18.4 ± 2.7^c
24-h maximum	48.8 ± 3.5^a	42.9 ± 3.7^b	38.1 ± 3.9^c
24-h minimum	12.3 ± 4.1^a	14.2 ± 2.4^b	6.3 ± 5.2^c
24-h range	36.5 ± 4.8^a	28.7 ± 4.7^b	31.7 ± 5.8^c
24-h WBGT index (°C)	18.7 ± 1.9^a	20.6 ± 1.2^b	15.6 ± 2.5^c
24-h water vapor pressure (kPa)	0.9 ± 0.4^a	2.0 ± 0.2^b	1.4 ± 0.3^c
24-h wind speed ($m \cdot s^{-1}$)	1.3 ± 0.3^a	0.9 ± 0.3^b	0.7 ± 0.3^c
24-h solar radiation ($W \cdot m^{-2}$)	285 ± 59^a	223 ± 62^b	187 ± 46^c
24-h maximum solar radiation ($W \cdot m^{-2}$)	1101 ± 115^a	1088 ± 164^a	807 ± 153^b
Total rainfall (mm)	77	784	70
Time of sunrise	$06:09 \pm 0:05^a$	$06:40 \pm 0:13^b$	$07:08 \pm 0:05^c$
Time of solar noon	$11:42 \pm 0:06^a$	$12:03 \pm 0:03^b$	$11:52 \pm 0:02^c$
Time of sunset	$19:15 \pm 0:13^a$	$19:26 \pm 0:14^b$	$18:35 \pm 0:10^c$
Photoperiod (h)	13.1 ± 0.2^a	12.5 ± 0.3^b	11.3 ± 0.2^c

Values in the same row with different superscript letters differed significantly ($P < 0.05$, ANOVA). WBGT, wet-bulb globe temperature.

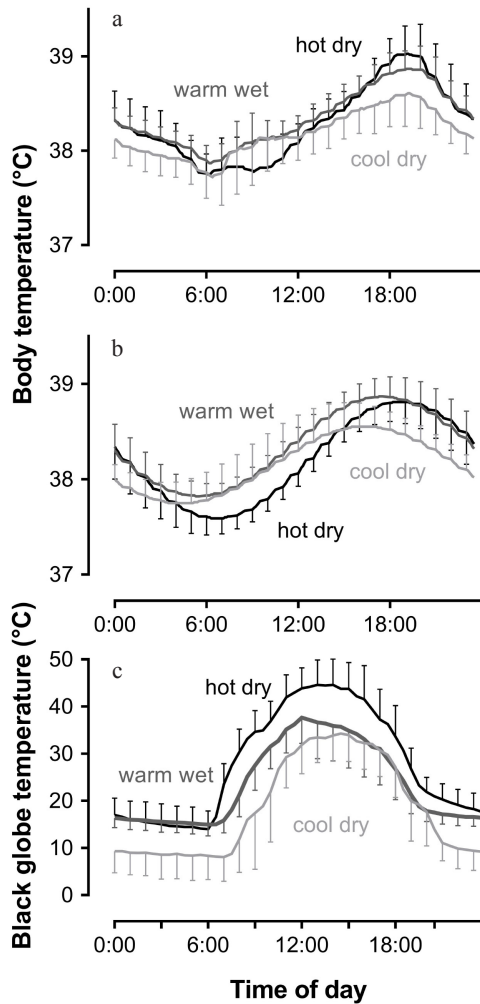


Figure 1 Nychthemeral rhythm of body temperature (mean \pm SD), averaged for all 5 free-living cheetahs, from original body temperature records (a) and cosinor rhythms (b) and the prevailing black globe temperatures (c) over the 3 seasonal periods. The cheetahs demonstrated a nychthemeral rhythm of body temperature that was not in phase with the globe temperature.

different from the range in the hot-dry seasonal period (2.4 ± 0.2 °C). There was no difference in absolute maximum body temperature between seasonal periods (Table 2). The times at which the minimum and maximum body temperatures occurred moved nearer to sunrise as the seasons progressed (Table 2), but those times since sunrise occurred at the same percentage of photoperiod

(minimum $10\% \pm 3\%$, maximum $90\% \pm 5\%$) irrespective of seasonal period.

The cosinor curves that we fitted to the body temperature data had an $r^2 = 0.53 \pm 0.07$, confirming that cosinor curves were valid representations of the underlying body temperature rhythms. Analysis of the cosinor curves showed no difference in the mesor or minimum of the cosinor body temperature rhythm between the 3 seasonal periods, but a significantly larger amplitude of the cosinor body temperature rhythm in the hot-dry period than in the other 2 periods (Table 2). The larger amplitude of the cosinor body temperature rhythm in the hot-dry period resulted in a higher maximum of the cosinor body temperature rhythm in that period than in the cool-dry period ($P < 0.01$). While the amplitude is symmetrical about the mesor, the slightly lower mean value of the mesor (although not significantly so) combined with smaller mean amplitude of the cosinor body temperature rhythm resulted in a significantly lower maximum of the cosinor body temperature rhythm in the cool-dry period than in both the hot-dry ($P < 0.01$) and the warm wet ($P < 0.05$) periods. The acrophase of the cosinor body temperature rhythm was later in the hot-dry period than in both the warm-wet ($P < 0.05$) and cool-dry ($P < 0.01$) periods (Table 2).

Across the whole study period, the minimum 24-h body temperature increased with increasing minimum 24-h black globe temperature, decreased with increasing wind speed, and was independent of rainfall (Table 3). The maximum 24-h body temperature was associated positively with wet bulb globe temperature and maximum activity (Table 3). The time of maximum body temperature became later when the days were longer (photoperiod) and was associated positively with the time of maximum activity, but was independent of the time of maximum black globe temperature (Table 3). The range of 24-h body temperature rhythm was associated positively with the 24-h range of black globe temperature and the maximum 24-h activity (Table 3).

Activity

There was a nychthemeral rhythm in the general locomotor activity of the cheetahs; that is, the activity excluding hunts. The activity rhythm had a shape different from that of the body temperature rhythm, and the activity rhythm varied much more than did the temperature rhythm between seasonal periods (Fig. 2). The total 24-h activity, the maximum 24-h activity and the timing of that maximum activity did not differ seasonally (Table 4). Locomotor activity occurred primarily in day-

Table 2 24-h body temperature variables (mean \pm SD) and the cosinor rhythms of 5 free-living cheetahs during the 3 seasonal periods

	Hot-dry (October–December)	Warm-wet (January–March)	Cool-dry (April–May)	Statistics
Body temperature (°C)				
24-h mean	38.3 \pm 0.3	38.3 \pm 0.2	38.2 \pm 0.2	$F_{2,8} = 1.9, P = 0.21$
24-h minimum	37.2 \pm 0.3	37.3 \pm 0.1	37.3 \pm 0.3	$F_{2,8} = 0.89, P = 0.45$
24-h maximum	39.6 \pm 0.3 ^a	39.5 \pm 0.2 ^a	39.2 \pm 0.3 ^b	$F_{2,8} = 8.6, P = 0.01$
24-h range	2.4 \pm 0.2 ^a	2.2 \pm 0.2 ^{a,b}	2.0 \pm 0.2 ^b	$F_{2,8} = 14.1, P = 0.002$
Absolute maximum	40.9 \pm 0.4	40.8 \pm 0.2	40.4 \pm 0.5	$F_{2,8} = 3.5, P = 0.08$
Time of minimum (time of day)	7:55 \pm 0:40	8:05 \pm 0:30	7:55 \pm 0:30	$F_{2,8} = 0.10, P = 0.91$
Time of minimum (time after sunrise)	01:45 \pm 0:43 ^a	01:20 \pm 0:30 ^{a,b}	0:46 \pm 0:42 ^b	$F_{2,8} = 4.39, P = 0.05$
Time of minimum (% of photoperiod)	14 \pm 6	11 \pm 4	7 \pm 6	$F_{2,8} = 3.00, P = 0.11$
Time of maximum (time of day)	18:30 \pm 0:30 ^a	17:55 \pm 0:35 ^{a,b}	17:20 \pm 0:55 ^b	$F_{2,8} = 8.5, P = 0.01$
Time of maximum (time after sunrise)	12:18 \pm 0:28 ^a	11:12 \pm 0:40 ^b	10:10 \pm 1:20 ^c	$F_{2,8} = 27.5, P = 0.0003$
Time of maximum (% of photoperiod)	94 \pm 1	88 \pm 1	89 \pm 1	$F_{2,8} = 2.56, P = 0.17$
Cosinor rhythm (°C)				
Mesor	38.3 \pm 0.3	38.3 \pm 0.2	38.2 \pm 0.2	$F_{2,8} = 1.9, P = 0.21$
Minimum	37.6 \pm 0.2	37.8 \pm 0.1	37.7 \pm 0.2	$F_{2,8} = 1.3, P = 0.31$
Maximum	38.9 \pm 0.2 ^a	38.9 \pm 0.2 ^a	38.6 \pm 0.2 ^b	$F_{2,8} = 7.6, P = 0.01$
Amplitude	0.63 \pm 0.04 ^a	0.52 \pm 0.06 ^b	0.46 \pm 0.12 ^b	$F_{2,8} = 12.9, P = 0.003$
Acrophase (time of day)	18:45 \pm 0:55 ^a	17:00 \pm 0:35 ^b	16:20 \pm 1:10 ^b	$F_{2,8} = 15.8, P = 0.002$

Values in the same row with different superscript letters differed significantly ($P < 0.05$, ANOVA). Bold text highlights significant seasonal effects.

Table 3 Generalized linear mixed-effects model (GLMM) results for the association between variables of the 24-h body temperature profiles of 5 free-living cheetahs and corresponding environmental and activity variables

	$\beta \pm$ SE	Z	P	95% Confidence interval of β
Minimum 24-h body temperature (°C)				
Minimum 24-h black globe temperature	0.016 \pm 0.004	4.3	<0.001	0.009–0.023
Wind speed	–0.136 \pm 0.047	–2.9	0.003	–0.227–0.045
Rainfall	0.002 \pm 0.002	1.2	0.22	–0.001–0.006
Maximum 24-h body temperature (°C)				
Wet-bulb globe temperature	0.042 \pm 0.012	3.3	0.001	0.017–0.066
Maximum 24-h activity	0.007 \pm 0.001	8.1	<0.001	0.005–0.008
Time of day of maximum 24-h body temperature				
Photoperiod	0.028 \pm 0.008	3.3	0.001	0.011–0.044
Time of maximum black globe temperature	0.155 \pm 0.084	1.8	0.07	–0.011–0.322
Time of day of maximum activity	0.076 \pm 0.019	4.0	<0.001	0.038–0.113
Range of 24-h body temperature rhythm (°C)				
Range of black globe temperature	0.025 \pm 0.006	4.4	<0.001	0.014–0.036
Maximum 24-h activity	0.009 \pm 0.001	8.5	<0.001	0.007–0.011

Days since winter solstice nested within individual cheetah identities were included as random factors. Body mass and sex of individual cheetah were included as control variables. $N = 954$ days of body temperature and climatic data for the 24-h body temperature model and 571 days of activity data for all other models. Bold text highlights significant associations at a 0.05 significance level.

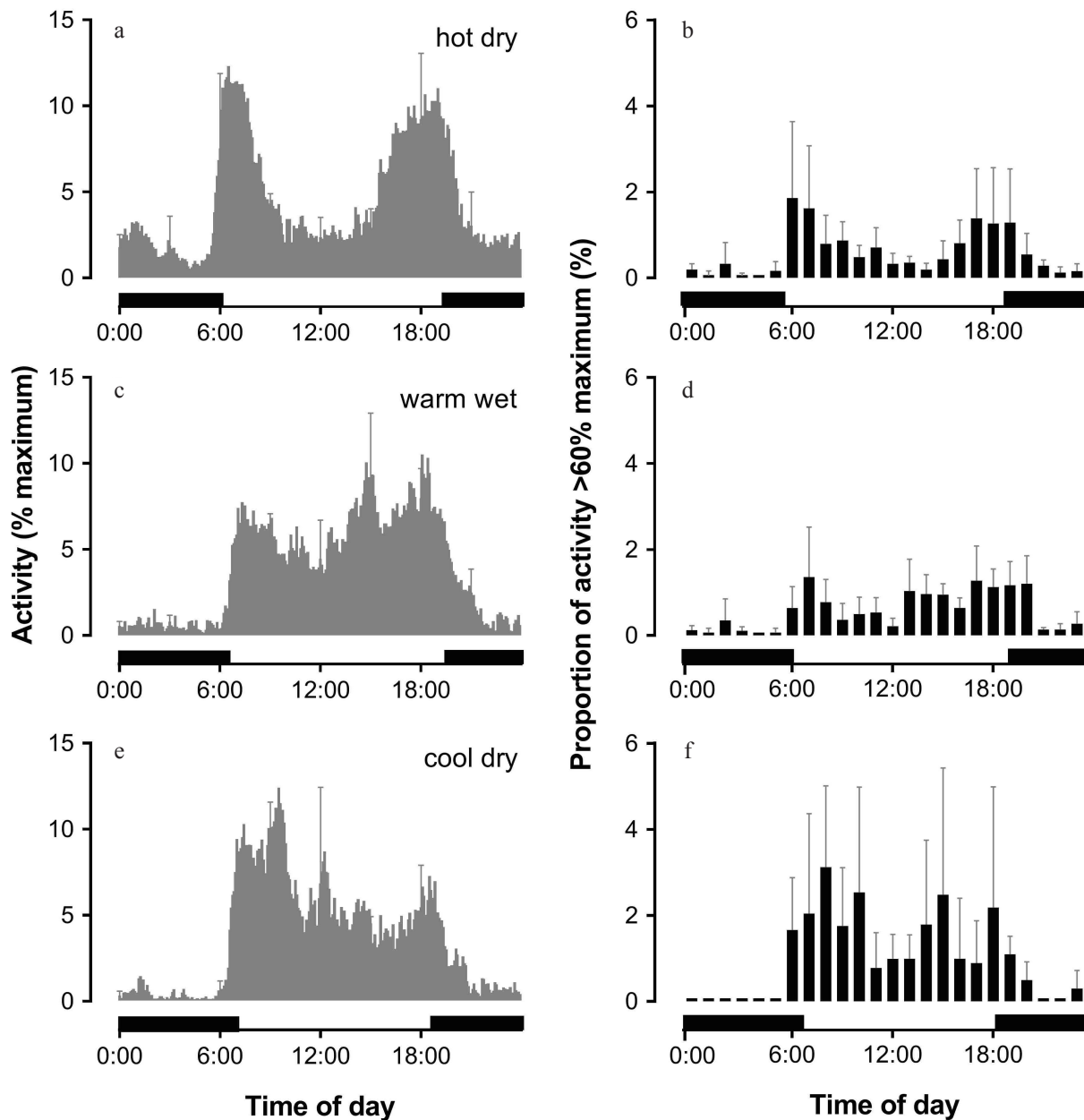


Figure 2 Mean locomotor activity in each 5-min epoch over the 24-h day excluding hunt activity (left panels) and the proportion of time spent in a hunting chase during each hour of the day (defined as activity levels higher than 60% of the maximum recorded per logger, right panels) in free-living cheetahs ($n = 5$ hot dry, $n = 3$ warm wet, $n = 2$ cool dry). The cheetahs shifted from continuous activity with crepuscular peaks during the hot-dry period (panel a) to predominantly diurnal activity, without clear crepuscular peaks, during the warm-wet (panel c) and the cool-dry (panel e) periods. The hunt profile followed a similar pattern, with cheetahs hunting primarily at dawn and dusk during the hot-dry period (panel b) and throughout the day during the warm-wet (panel d) and the cool-dry (panel f) periods, but there were nocturnal hunts in the hot-dry and warm-wet periods. Activity was biologged over 5-min epochs, and is shown as the percentage of the maximum reading for each logger at any time after implantation (to account for sensitivity differences between loggers). Horizontal bars indicate night.

light, but there was some nocturnal activity in each of the seasonal periods. In a 24-h period, a cheetah could undertake all its activity between sunrise and sunset or could undertake all its activity between sunset and sunrise. The proportion of nocturnal activity (between sunset and sunrise) for 24-h periods was independent of seasonal period (Table 4) and averaged $26 \pm 12\%$ for the study period, but how activity was distributed through the daylight hours did differ between seasonal periods. In the hot-dry seasonal period, activity was attenuated during the heat of the day, leaving clear crepuscular

peaks in activity (Fig. 2a). Those peaks were less pronounced in the cooler seasons, with cheetahs typically active throughout the daylight hours (Fig. 2c,e). Consequently, a significantly greater proportion of total activity took place between 0900 and 1500 hours (the hottest 6 h of the day centered on solar noon) in the cool-dry period than in the hot-dry period (Table 4). Indeed, in the cool-dry period most of the cheetahs' diurnal activity took place in the hottest 6 h of the day.

The total 24-h activity was not associated with the maximum 24-h black globe temperature nor photoperi-

Table 4 Total 24-h locomotor activity variables (mean \pm SD) of 5 free-living cheetahs during the 3 seasonal periods

	Hot-dry October–December (<i>n</i> = 5)	Warm-wet January–March (<i>n</i> = 3)	Cool-dry April–May (<i>n</i> = 2)	Statistics
Activity				
Total 24-h activity	1400 \pm 410	1230 \pm 73	1240 \pm 135	$F_{2,7} = 0.43, P = 0.67$
Maximum 24-h activity	68 \pm 13	64 \pm 5	63 \pm 8	$F_{2,7} = 0.04, P = 0.96$
Time of maximum activity	12:53 \pm 1:26	14:12 \pm 0:08	12:17 \pm 0:26	$F_{2,7} = 2.81, P = 0.13$
Proportion activity between sunset and sunrise (% total)	29 \pm 13	19 \pm 5	23 \pm 6	$F_{2,7} = 1.07, P = 0.39$
Proportion activity between 0900 and 1500 hours (% total)	18 \pm 9 ^a	32 \pm 11 ^{a,b}	40 \pm 15 ^b	$F_{2,7} = 5.14, P = 0.04$

Values in the same row with different superscript letters differed significantly ($P < 0.05$, ANOVA). Bold text highlights significant seasonal effects.

Table 5 Generalized linear mixed-effects model (GLMM) results for the association between variables of the 24-h activity profiles of 5 free-living cheetahs and corresponding environmental variables

	$\beta \pm$ SE	<i>Z</i>	<i>P</i>	95% confidence interval of β
Total 24-h activity				
Photoperiod	118 \pm 99	1.2	0.23	-76–312
Maximum 24-h black globe temperature	1.0 \pm 12.3	0.08	0.93	-23–25
Time of day of maximum activity				
Photoperiod	0.03 \pm 0.02	1.3	0.18	-0.014–0.075
Maximum 24-h black globe temperature	-0.005 \pm 0.002	-1.8	0.08	-0.010–0.0005
Proportion of nocturnal activity				
Photoperiod	-0.036 \pm 0.021	-1.7	0.09	-0.078–-0.006
Maximum 24-h black globe temperature	0.006 \pm 0.003	2.5	0.01	0.001–0.012
Phase of the moon	0.12 \pm 0.04	3.3	0.001	0.049–0.189
Proportion of activity between 0900 and 1500 hours				
Photoperiod	-6.2 \pm 2.2	-2.8	0.005	-10.6–-1.8
Maximum 24-h black globe temperature	-0.81 \pm 0.28	-2.9	0.004	-1.4–-0.3

Note: Days since winter solstice nested within individual cheetah identities were included as random factors. Body mass and sex of individual cheetah were included as control variables. $N = 571$ days. Bold text highlights significant associations at a 0.05 significance level.

od (Table 5). Similarly, the time of maximum activity, presumably hunting, was not associated with the maximum 24-h black globe temperature nor photoperiod (Table 5). The proportion of activity that took place between 0900 and 1500 hours was associated inversely with maximum 24-h black globe temperature and photoperiod (Table 5). The proportion of activity that took place at night was associated positively with the maximum 24-h black globe temperature but was not associated with photoperiod. A non-thermal factor, phase of the moon, was also associated with the proportion of activity that took place at night (Table 5); the proportion of activity that took place at night was higher on moonlit nights. Despite that preference for moonlit nights, on 3 occasions cheetahs displayed high levels of activity

(presumably hunts) on moonless (new moon) nights (e.g. Fig. 3b). Based on the body temperature profile following the high levels of activity on moonless nights, 1 of the 3 of these hunts was successful.

Hunts

The distribution of chases during putative hunts (defined as epochs of activity >60% of maximum activity) during each hour over the 24-h day (Fig. 2b,d,f) looked very similar to the distribution of other locomotor activity. The proportion of time in which epochs of activity exceeded 60% per hour correlated positively with the general activity within that hour, per seasonal period ($r^2 > 0.64$, $P < 0.0001$). The total number of hunts per day and the number of successful hunts per day were both

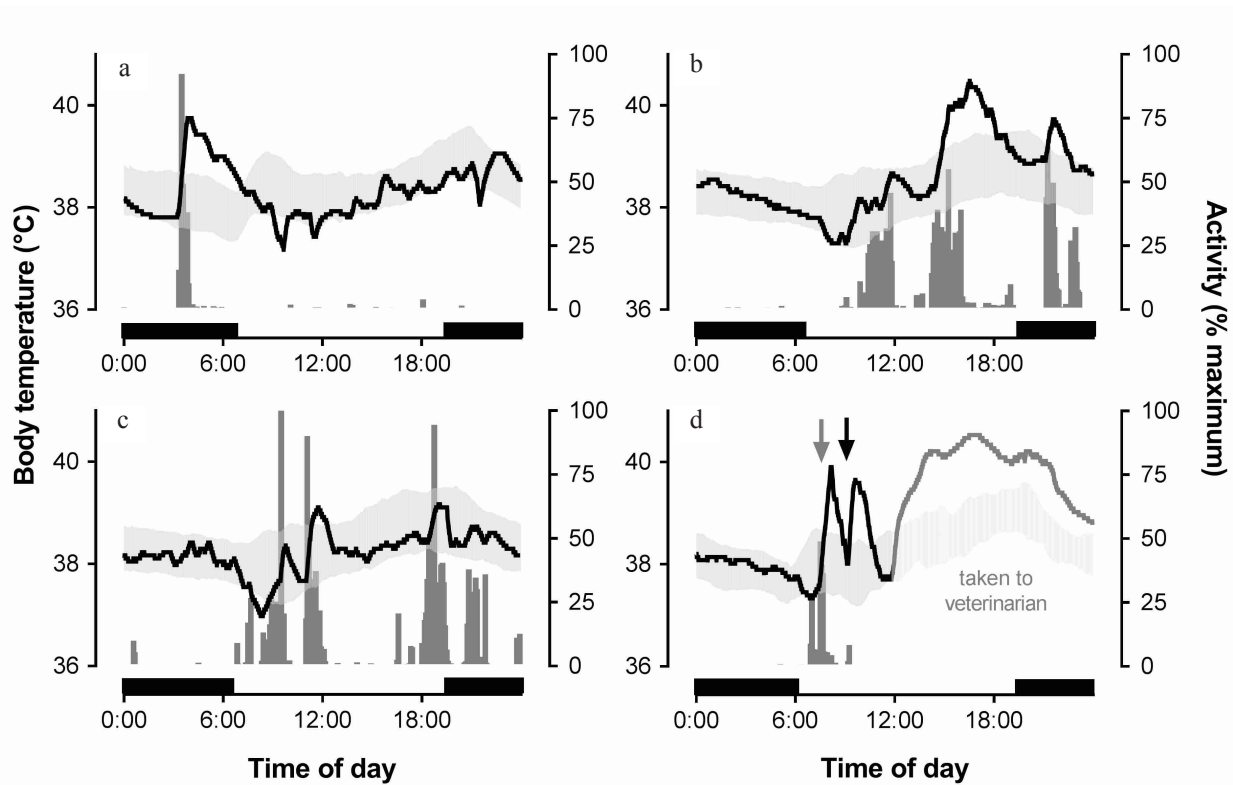


Figure 3 24-h body temperature (solid black line) and activity (grey vertical bars) patterns for 3 free-living cheetahs on separate occasions. Horizontal black bars indicate night. Grey bands indicate the nychthemeral body temperature rhythm (mean \pm SD) for each cheetah during the corresponding seasonal period. The upper panels show the body temperature and activity profile of 2 free-living female cheetahs when the cheetahs appear to have hunted at night during both full moon (female 1, panel a) and new moon (female 2, panel b). The lower panels show a day when 1 of the female cheetahs (female 1, panel c) hunted at midday when black globe temperature exceeded 52 °C and a day when 1 of the male cheetahs (male 4, panel d) was attacked by a resident leopard *Panthera pardus*. The grey arrow indicates the time of the hunt of an adult impala (0730 hours). Two hours later the leopard attacked the cheetah and severed his spine (black arrow). We took the cheetah to the local veterinarian for treatment, but he had to be euthanized the following day.

associated positively with the general 24-h activity (Table 6). The number of hunts per night was not associated with either the photoperiod or phase of the moon (Table 6). Rather, cheetahs were more likely to hunt at night at times when they were otherwise active at night, which, in turn, was associated with moonlight and globe temperatures, but moonlight and globe temperature did not independently affect nocturnal hunts. Based on the occurrence of epochs with activity levels above 60%, our cheetahs hunted between 1 and 3 times per day (1.2 ± 0.9 hunts per day). Cheetahs were successful in taking down prey in $38\% \pm 15\%$ of the attempted hunts, as determined from activity and body temperature profiles, with the 2 male cheetahs that had prior hunting experience having the best hunting success (52% for male 1 and 56% for male 2). Although most putative hunts took place in daylight hours, hunts were not confined to the day (Fig. 2), with $22\% \pm 15\%$ of hunts taking place between sunset and sunrise. We recorded 95 putative hunts between 20:00 and 05:00 hours; that is, hunts that were clearly not diurnal or crepuscular (e.g. Fig. 3a). Female 2 engaged in 40 such hunts (9% of her hunts) during the 7-month study period.

The success of a hunt was not affected by the black globe temperature at the time of the hunt (Fig. 4a) nor

by the time of day (Fig. 4b). We recorded 81 occasions when cheetahs hunted at times when black globe temperature exceeded $40\text{ }^{\circ}\text{C}$ and, on occasion (Fig. 3c), cheetahs hunted when black globe temperatures exceeded $52\text{ }^{\circ}\text{C}$ (air temperature $33.6\text{ }^{\circ}\text{C}$). GLMM analysis (Table 6) confirmed that neither the number of hunts per day nor the number of successful hunts was associated with maximum 24-h black globe temperature.

Discussion

As far as we are aware, this is the first study to report continuous and concurrent long-term measurements of body temperature and activity data for any free-living felid. Despite the cheetahs being exposed to air temperatures below freezing in winter and close to $40\text{ }^{\circ}\text{C}$ in summer (with black globe temperatures reaching $56\text{ }^{\circ}\text{C}$), biologging technology showed that the cheetahs maintained their body temperature within a relatively narrow 24-h range of approximately $2.3\text{ }^{\circ}\text{C}$, within the range of that observed for large herbivores (Hetem *et al.* 2016). On average, the body temperature of our cheetahs ranged between 37.2 and $39.6\text{ }^{\circ}\text{C}$, similar to that reported for captive cheetahs ($39\text{--}40\text{ }^{\circ}\text{C}$; Taylor & Rowntree 1973) and other felids ($37.0\text{--}38.4\text{ }^{\circ}\text{C}$; Mc-

Table 6 Generalized linear mixed-effects model (GLMM) results for the association between variables of the 24-h hunting profiles of 5 free-living cheetahs and corresponding environmental and activity (excluding hunts) variables

	$\beta \pm \text{SE}$	Z	P	95% confidence interval
Total number of hunts per day				
Photoperiod	-0.02 ± 0.10	-0.15	0.88	-0.22–0.19
Maximum 24-h black globe temperature	-0.001 ± 0.013	-0.11	0.91	-0.03–0.02
Total 24-h activity (excluding hunts)	0.0007 ± 0.00006	12.9	<0.001	0.0006–0.0008
Number of successful hunts per day				
Photoperiod	0.04 ± 0.16	0.2	0.82	-0.27–0.34
Maximum 24-h black globe temperature	0.01 ± 0.02	0.7	0.50	-0.02–0.05
Total 24-h activity (excluding hunts)	0.0005 ± 0.0001	5.9	<0.001	0.0003–0.0007
Number of hunts per night				
Photoperiod	0.27 ± 0.25	1.1	0.28	-0.22–0.76
Maximum 24-h black globe temperature	-0.01 ± 0.03	-0.3	0.79	-0.07–0.05
Phase of the moon	0.49 ± 0.43	1.1	0.26	-0.36–1.3
Proportion nocturnal activity (excluding hunts)	3.00 ± 0.49	9.1	<0.001	2.04–3.97

Note: Days since winter solstice nested within individual cheetah identities were included as a random factor. Body mass and sex of individual cheetah were included as control variables. $N = 571$ days and 337 days on which hunts occurred. Bold text highlights significant associations at a 0.05 significance level.

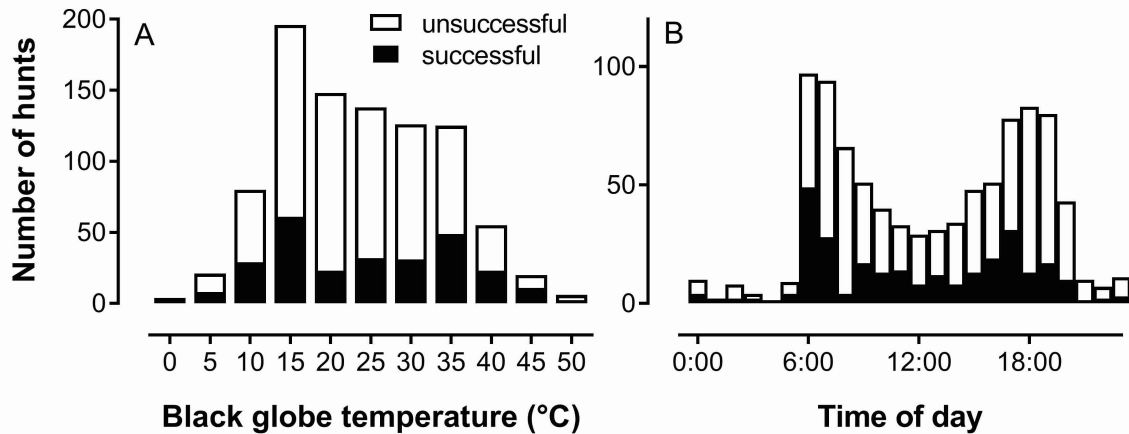


Figure 4 The total number of successful and unsuccessful hunts for all 5 free-living cheetahs across different ambient temperatures (panel A) and times of day (panel B). Based on body temperature profiles during observed hunts of the same cheetahs (Hetem *et al.* 2013), chases were defined as an activity level higher than 60% of the maximum recorded per logger and the chase was classified as successful if body temperature increased by more than 0.5 °C within 30 min of the spike of activity that identified the time of the chase.

Nab 2000), including free-living lions (36–39 °C; Trethowan *et al.* 2017). Although felids have been reported to have body temperatures higher than those of other mammals of similar body mass because of their unusually high metabolic rates (McNab 2000), the mean, minimum and maximum of the nycthemeral rhythms of body temperatures of our cheetahs fell within the 95% confidence intervals of regression lines fitted to the relationship between body temperature and body mass for 17 species of free-living mammalian herbivores (Hetem *et al.* 2016). Indeed, the body temperature rhythms of our cheetahs were remarkably similar to those of their ungulate prey exposed to similar environmental conditions in southern Africa (Fuller *et al.* 2000; Maloney *et al.* 2002; Hetem *et al.* 2008; Shrestha *et al.* 2012).

Contrary to our hypothesis, seasonal periods had little influence on the cheetahs' body temperature and rhythm, despite the hot-dry period being characterized by high wind speeds and average black globe temperatures that were 10 °C higher than those in the cool-dry period, and both water vapor pressure and rainfall that was higher in the warm-wet than the other 2 periods. The mean and minimum 24-h body temperature did not differ significantly across seasonal periods. The maximum 24-h body temperature, however, was approximately 0.4 °C higher during the hot-dry period than during the cool-dry period. The higher maximum in the hot-dry period

was not the consequence of short, hyperthermia-inducing events occurring in that seasonal period because it was evident in the cosinor analysis too. We presume that it was associated with the higher ambient temperatures of that period. The higher maximum did lead to a larger range of the 24-h rhythm of body temperature in the hot-dry period that was statistically significant, but it is likely too small to be of any real biological significance. Other than as a result of differences in photoperiod, the timing of the maxima or minima of body temperature did not differ seasonally. The thermal status of the day itself had a stronger influence on body temperature than did seasonal period. Maximum 24-h body temperature was influenced not just by environmental heat but also by activity, with the magnitude and the timing of the maximum 24-h body temperature being associated with the magnitude and timing of the maximum 24-h activity, and maximum activity was associated with hunts.

Despite their reportedly high metabolic rate (McNab 2000), the high metabolic load of hunting (Taylor *et al.* 1974), and being active at very high ambient temperatures, our cheetahs usually maintained homeothermy, which implies that they were able to dissipate excess heat effectively. The cheetah's nasal anatomy allows for effective evaporative cooling (Torregrosa *et al.* 2010), provided that the vapor pressure of the air is sufficiently low. We frequently observed our cheetahs hyperventi-

lating, presumably panting, even when inactive. We observed our cheetahs drinking on 12 occasions, including 1 instance where a female cheetah drank shortly after consuming a kill, implying that not all water needs were met by the water content (tissues, blood and urine) of the prey. Cheetahs exhibit behaviors that reduce the requirement for evaporative cooling. When they can, they avoid high heat loads by seeking shade (Schaller 1968; Saleh *et al.* 2001; Skinner & Chimimba 2005) and resting on hot days (Bothma & Walker 1999). In addition to their favored termite mounds (Bothma & Walker 1999), cheetahs select rocky outcrops (kopjes) as vantage points (Caro & Collins 1987; Pettorelli *et al.* 2009), potentially for their access to shade (Hilborn *et al.* 2012) and exposure to wind.

Not only were cheetahs able to prevent excessive rises in body temperature, but they were also able to sustain relatively high minimum 24-h body temperatures, despite ambient temperatures below freezing on occasion. Captive cheetahs may be thermally stressed on cold days as they display elevated corticosterone production at low air temperatures (Uetake *et al.* 2014). In a high-altitude habitat, free-living cheetahs preferred locations with more solar radiation (Welch *et al.* 2015), although such behavior will not help them maintain homeothermy at night. Based on our observations of large herbivores (Hetem *et al.* 2016), we would have expected the minimum 24-h body temperature to have been lower in seasonal periods when the cheetahs would have been in energy deficit. That there was no change in the minimum body temperature across the periods suggests that the cheetahs apparently were not energetically challenged during the study period, a conclusion supported by their maintenance of hunting success irrespective of weather.

The only substantial departures from the regular nycthemeral rhythm of body temperature were related to hunts. The maxima in the 24-h body temperature rhythms often were those peaks after successful hunts, and, indeed, the timing of the maximum 24-h body temperature events was associated statistically with the time of maximum activity. The hyperthermia was not associated with the intensity of the chase or with feeding, but probably arose as a result of stress-induced hyperthermia linked to high sympathetic nervous system activity associated with vulnerability to attack and kleptoparasitism by more dominant intraguild predators (Hetem *et al.* 2013).

It is avoiding those predators that has been the explanation advanced historically for the contention that

cheetahs are one of the few felids to exhibit primarily diurnal activity (Estes 1991; Skinner & Chimimba 2005). The idea that cheetahs are diurnally active stems from traditional behavioral observations, which were heavily biased towards observations made during daylight hours. Biologgers, which can record activity remotely and continuously, have revealed that cheetahs exhibit an unexpectedly high level of nocturnal activity (Fig. 2). Indeed, approximately one-quarter of our cheetahs' activity occurred between sunset and sunrise (Table 4). The proportion of nocturnal activity was highest on moonlit nights and when daytime ambient temperatures were high. Other researchers have recently cast doubt on the idea that cheetahs avoid all activity at night; they report that between 25% and 46% of cheetah 24-h activity (Hayward & Slotow 2009; Cozzi *et al.* 2012; Broekhuis *et al.* 2014) and up to 46% of kills made (Bissett & Bernard 2007) occurred at night. In extreme thermal environments, such as the Sahara Desert where air temperatures exceed 40 °C, the Saharan cheetah (*Acinonyx jubatus hecki* Hilzheimer, 1913) is active almost exclusively at night (Belbachir *et al.* 2015).

Cheetahs are sometimes reported as being crepuscular (Durant 1998; Bissett & Bernard 2007; Hayward & Slotow 2009; Grünewälder *et al.* 2012). In some regions cheetahs show a preference for hunting at dawn (Cozzi *et al.* 2012), with more than half of all hunts occurring between 0600 and 1000 hours (Schaller 1968; Wilson *et al.* 2013). In the hot-dry seasonal period, heat stress apparently prevented our cheetahs being equally active throughout the daylight hours (Fig. 2). The proportion of activity that occurred in the hottest part of the day, between 0900 and 1500 hours, in the hot-dry seasonal period was half of that recorded in the other seasonal periods (Table 4), which was similar to the patterns of activity observed in Kalahari cheetahs (Mills & Mills 2017). Shifting activity to cooler crepuscular periods of the day compensated for the effects of decreased activity during the heat of the day, and total 24-h activity was not influenced by maximum 24-h ambient temperature. Others have reported that high ambient temperatures are associated with reduced activity levels in cheetahs and African wild dogs *Lycan pictus* Temminck, 1820 during the day (Cozzi *et al.* 2012; Woodroffe *et al.* 2017). Cheetahs in the Okavango delta spent more time hunting at night during the dry season than during the wet season (Broekhuis *et al.* 2014) and these seasonal differences were particularly evident in female cheetahs (Grünewälder *et al.* 2012). However, wet-season effects may be related more to moonlight than to rainfall as the moon would have been obscured by clouds. In-

deed, the proportion of nocturnal activity of cheetahs increased from 15% on new-moon nights to 40% on full moon nights (Cozzi *et al.* 2012). Some have suggested that cheetahs are active at night only if there is sufficient light (Cozzi *et al.* 2012). Yet cheetahs are capable of hunting in total darkness (Stander 1990; Mills & Mills 2017), and, on occasion, our cheetahs hunted, sometimes successfully, on moonless nights (Fig. 3b).

Consistent with our hypothesis about when cheetahs hunt, the main factor that was associated with the timing of hunts in our cheetahs was the timing of general activity. They hunted when they were already on the move. The number of hunts and the number of successful hunts over 24-h periods was associated with the level of non-hunt activity over 24 h, and the number of nocturnal hunts with the proportion of non-hunt activity that was nocturnal (Table 6). An alternative explanation is that the cheetahs went on the move when they were hungry and needed to hunt. That explanation would not fit with the seasonal changes in activity that we observed; for example, we have no reason to believe that cheetahs were hungrier between 0900 and 1500 hours in the cool-dry seasonal period than at the same time in other seasonal periods, but they were more active then. Similarly, the hunger level of cheetahs in east Africa did not influence their decision to hunt (Cooper *et al.* 2007). It seems as if the cheetahs would attempt to hunt if they came across potential prey while they were active. Our data showed that the cheetahs were prepared to hunt, and were equally successful, whatever the weather conditions. It was never too hot to hunt, if the cheetahs were active at the time. However, it could be too hot to be active.

The hunting patterns of our cheetahs were similar to those reported in the literature, despite our cheetahs being part of a rehabilitation program and 3 of our 5 cheetahs having had no prior hunting experience at the start of the study. Further support for our rehabilitated cheetahs being representative of wild cheetahs comes from their prey selection. The prey of our cheetahs, as identified after some hunts (Table S1), was not unexpected given that cheetahs preferentially select medium-sized (<60 kg) prey (Schaller 1968; Mills *et al.* 2004; Hayward *et al.* 2006) with non-random selection for juveniles of medium to large prey (Schaller 1968; Pienaar 1969; Mills *et al.* 2004). Potentially, the unusually high rainfall that occurred at the study site may have been stressful for our cheetahs (Uetake *et al.* 2014) as it would have changed the vegetation structure and density throughout the course of the study, a factor for which

we were unable to account in our analyses. However, cheetahs hunt successfully in dense vegetation with little difference in hunt distance or speed reached within different habitats (Wilson *et al.* 2013). Our study area was only a fraction of the size of home ranges reported for free-ranging cheetah (Broomhall *et al.* 2003; Marker *et al.* 2008), but similar to the approximately 40-km² core areas generally used (Marnewick & Somers 2015). We do not believe the small study area adversely impacted the general activity of the cheetahs or our results. A limitation of our study was that we drew some conclusions about behavior from 3 of our cheetahs (the siblings) which hunted as a coalition for most of the data collection period, and we lost 2 cheetahs before the study was complete. In addition, we observed 28 hunts and found the cheetahs on an additional 35 kills; we derived hunt occurrence, and their success, from characteristic profiles of body temperature that we had identified previously from hunts that we had observed directly (Hetem *et al.* 2013). In our analysis of the biologged data we probably missed a few hunts and misclassified a few hyperthermic episodes as hunts, but those false negatives and positives would have been distributed randomly and so were unlikely to have distorted the trends that we observed. Our calculation that between 21% and 52% of our cheetahs' hunts were successful provides some support for our model validity as these values fall within the range of hunt success rates previously reported for cheetah (Schaller 1968; Eaton 1970; Mills *et al.* 2004; Bissett & Bernard 2007; Hilborn *et al.* 2012; Wilson *et al.* 2013).

Although we have shown that thermal factors play a role in cheetah activity, the reduced risk of encountering larger, more dominant predators, which are primarily nocturnal (Hayward & Slotow 2009), remains a compelling explanation for cheetahs to avoid nocturnal activity. When cheetahs engage in high nocturnal activity, their activity times do overlap with those of more dominant intraguild predators (Hayward & Slotow 2009; Cozzi *et al.* 2012). Cheetahs show higher levels of nocturnal activity on reserves without lions than on reserves where lions are present (Bissett *et al.* 2015), which may account for the high levels of nocturnal activity observed in our cheetahs. Probably to the cheetahs' detriment, the thermal factors that lead to cheetahs engaging in nocturnal activity also influence the more dominant predators to become nocturnal. Lions, *Panthera leo* Linnaeus, 1758 (Hayward & Hayward 2007), reduce their diurnal activity during hot summer months. Spotted hyenas, *Crocuta crocuta* Erxleben, 1777, have been report-

ed to not hunt at air temperatures above 20 °C (Cooper 1990) and are inactive during the heat of the day (Hayward & Hayward 2007). Wild-born cheetahs lose up to 13% of their prey to kleptoparasitism (Schaller 1968; Mills *et al.* 2004; Hunter *et al.* 2007a,b; Scantlebury *et al.* 2014). Kleptoparasitism is more frequent at night, perhaps resulting in shorter feeding bouts of cheetahs at night than during the day (Broekhuis *et al.* 2014). Indeed, all 4 of the kills observed on moonless nights by cheetahs in a Namibian reserve were lost to larger predators (Stander 1990). That our cheetahs preferred moonlit nights, on those occasions on which they did hunt at night, may be related to the avoidance of kleptoparasitism too. Lions and leopards both have improved hunting success on darker nights (Martins & Harris 2013). Not only do cheetahs lose their prey to more dominant carnivores, but they may themselves be vulnerable to predation. Although cubs are primarily targeted (Laurenson 1994), adult cheetahs are occasionally killed by both lions and leopards (Pienaar 1969; McVittie 1979; Bothma & Walker 1999; Durant 2000). Although our orphan cheetahs learned to hunt on their own after release into the wild, what they apparently did not learn on their own was to concede prey to the more dominant predators; 2 succumbed to leopard attacks. One of these attacks occurred soon after a hunt during the day (Fig. 3d).

In conclusion, biologging allowed us to study free-living cheetahs in their natural habitat, and doing so enabled us to draw new conclusions about cheetah biology. Biologging, particularly because it provides continuous data independent of the vagaries, and confounding influences, of human observers, gives us better insight into the biology of animals in their natural habitats than do traditional techniques. We believe that the use of biologging will soon become obligatory for research in wildlife biology.

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