

Getting to the core: internal body temperatures help reveal the ecological function and thermal implications of the lions' mane

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1. Abstract

It has been proposed that there is a thermal cost of the mane to male lions, potentially leading to increased body surface temperatures (T_s), increased sperm abnormalities, and to lower food intake during hot summer months. To test whether a mane imposes thermal costs on males, we measured core body temperature (T_b) continuously for approximately one year in 18 free-living lions. There was no difference in the 24 h maximum T_b of males ($n = 12$) and females ($n = 6$), and males had a 24 h mean T_b that was 0.2 ± 0.1 °C lower than females after correcting for seasonal effects. Although feeding on a particular day increased 24 h mean and 24 h maximum T_b , this phenomenon was true of both male and female lions, and females had higher 24 h mean and 24 h maximum T_b than males, on both days when lions did not feed, and on days when lions did feed. Twenty four hour T_b was not influenced by mane length or colour, and 24 h mean T_b was negatively correlated with mane length. These data contradict the suggestion that there exists a thermal cost to male lions in possessing a long dark mane, but do not preclude the possibility that males compensate for a mane with increased heat loss. The increased insulation caused by a mane does not necessarily have to impair heat loss by males, which in hot environments is primarily through respiratory evaporative cooling, nor does it necessarily lead to increased heat gain, as lions are nocturnal and seek shade during the day. The mane may even act as a heat shield by increasing insulation. However, dominant male lions frequent water points more than twice as often as females, raising the possibility that male lions are increasing water uptake to facilitate increased evaporative cooling. The question of whether male lions with manes compensate for a thermal cost to the mane remains unresolved, but male lions with access to water do not have higher T_b than females or males with smaller manes.

Key words: body temperature, ecological function, *Panthera leo*, thermal biology

2. Introduction

The most striking feature of the male African lion (*Panthera leo*) is its mane. A thick, dark mane is thought to have advantages for males that possess it, though hypotheses vary as to which are the most important. Charles Darwin and others proposed that the lion's mane may provide a signal of fighting prowess to other males, helping to avoid unnecessary conflicts, and protecting the neck when conflicts do occur (Darwin, 1871, Schaller, 1972). Alternatively, the lion's mane may simply be ornamental and mate choice may be the driving evolutionary force and the primary ecological function of the mane, as suggested by the finding that females preferentially move toward model male lions with darker manes (West and Packer, 2002). Indeed, by selecting males with darker manes, female lions are indirectly selecting more mature, healthy males, with higher testosterone levels, which may be able to better provide for and protect their prides (West and Packer, 2002).

Sexually selected traits have obvious advantages, such as those listed above for the lion's mane, but without a cost to keep them honest all individuals in a population might develop them to a similar extent, neutralising the usefulness of the signal. Thus, for signals of fitness to be useful they must be associated with a cost to keep them honest; the necessity of this cost is known as the handicap principle (Zahavi, 1977). The cost of a lion's mane may be a thermal one. As early as 1908, Frederick Selous, the famous British hunter-naturalist, proposed that the primary factor influencing the size of a lion's mane was ambient temperature (Selous, 1908). More recently, West and Packer (2002) found that body surface temperatures (T_s) measured shortly after sunset were higher for male lions with manes than for females, and that those males with darker manes tended to have higher T_s than males with lighter or no manes. The high T_s of dark-maned lions may represent a cost, particularly during the hot months when the high T_s was linked to sperm abnormalities and reduced food intake (West and Packer, 2002). The costs of maintaining a dark mane in hot climates may outweigh the benefits, and male lions in warmer climates generally have smaller manes, as demonstrated for captive lions across latitudes in North America (Patterson et al., 2006), and the small-maned Asian lion in India (Barnett et al., 2007).

The evidence to date that a darker and heavier mane might incur a thermal cost is based on a single study of T_s of lions measured by infrared thermography (West and Packer, 2002), yet physiological performance is influenced by core body temperature (T_b), and not T_s . Higher T_s of one individual than of another at a particular time of day does not necessarily represent a higher T_b . External factors such as air temperature, as well as peripheral vasomotor control can influence T_s , and T_b and T_s are therefore not well correlated (Porter and Gates, 1969). Indeed, if environmental temperature is lower than T_b , as is likely after sunset when initial measurements were made, then a higher T_s may reflect a higher skin temperature, associated with greater peripheral vasodilation to dissipate heat and reduce body temperature. A higher T_s on the flanks of male lions may therefore reflect increased vasomotor control to direct peripheral blood flow away from the areas covered by the mane, and towards areas where heat can be more easily dissipated, such as the loins and flanks. It is important to measure both T_b and T_s continuously when attempting to assess whether an animal is increasing or decreasing dry heat loss.

If a large, dark mane indeed has a thermal cost in hot environments, then one might expect T_b to be higher in males than in females, and higher in males with longer and darker manes. Although such a pattern was inferred from measurements of T_s (West and Packer, 2002), T_s is influenced by external factors such as air temperature and radiation, by peripheral vasomotor control, and by the pelage structure, and it varies much more than does T_b (Porter and Gates, 1969). Body surface temperature is therefore not a good indication of T_b in all thermal states. To further investigate whether there is a thermal cost of the lion's mane, we measured T_b for approximately one year in 18 free-living lions (six females, 12 males), in a hot semi-arid environment where lions develop prominent manes. We compared the T_b (24 h mean and maximum) of male and female lions across different seasons, and T_b of lions with short and long manes, or dark and light manes. We also compared lion T_b on days when the animals fed and did not feed, as it also has been reported that males reduce food intake due to the interaction between the specific dynamic action of digestion and the thermal burden of the mane (West and Packer, 2002). If there is a thermal cost of the mane, resulting in increased heat gain or reduced

heat dissipation, it is possible that male lions may maintain a T_b no different to that of females, as a result of increased evaporative heat loss. To investigate this idea we also measured the frequency and duration of water intake in males and females, as increased evaporative heat loss likely would be associated with greater water intake.

3. Materials and methods

3.1 Ethical note

All animal procedures carried out in this study received appropriate approval from the University of Oxford Animal Welfare and Ethical Review Board and the University Veterinary Services Department. Procedures were also approved by the Animal Ethics Screening Committee of the University of the Witwatersrand (clearance certificate no. 2013/54/04). A veterinarian carried out the surgical procedures and project staff that handled animals during captures were qualified to do so by attendance at Zimbabwe's Physical and Chemical Capture of Wild Animals Course and held valid drugs licenses (Dangerous Drugs License No. 2014/16). Permission was granted from the landowner and conservancy management, following the ASAB/ABS recommendations for the Use of Animals in Research, for the capture and handling of the study animals.

3.2. Study site

This study took place at the Buby Valley Conservancy (BVC), a privately owned wildlife conservancy located in southern Zimbabwe. The BVC is approximately 3700 km² and is located in the lowveld region of Zimbabwe between latitudes 21.2° and 21.8° South, and longitudes 29.8° and 30.5° East, at an elevation of 500 - 600 m above sea level. The lowveld region is in one of the hottest and driest areas in Zimbabwe with summer temperatures regularly exceeding 40 °C, and mean annual rainfall between 2007 and 2012 was 351 ± 76 mm (du Preez, 2014). Buby Valley Conservancy is a fenced wildlife conservancy with a full complement of indigenous megafauna (du Preez, 2014) and contains one of Zimbabwe's largest lion populations. The BVC is a mesotrophic ecosystem characterised by mopane (*Colophospermum mopane*) woodland and scrubland.

3.3. Weather data

Weather data were measured using a portable weather station (HOBO® Weather Station Data Logger - H21-001, Onset Computer Corporation, Massachusetts USA) erected in an open area at the study site and programmed to log measurements at five minute intervals. Weather parameters measured included dry bulb air temperature, black globe temperature, relative humidity, solar radiation, wind speed, and wind direction. We used a standard rain gauge to measure daily precipitation.

The rate of heat exchange between an animal and its environment depends not only on dry bulb air temperature, but also on wind speed, solar radiation, long wave radiation, and water vapour pressure (Hetem et al., 2007). Black globe temperature integrates dry bulb air temperature, solar radiation and wind speed and therefore provides a better measure of the factors which influence an animal's thermal balance than does dry bulb air temperature (Hetem et al., 2007). We therefore used black globe temperature instead of dry bulb air temperature in most of our analysis, but have included reference to dry bulb air temperature when we have described the environment. Seasonal weather conditions are summarised in supplementary data table S.1.

3.4. Bio-loggers

In this study, we used a combination of GPS satellite radio-telemetry collars, miniature temperature-sensitive bio-loggers, accelerometer bio-loggers, and acoustic-accelerometer bio-loggers. To monitor study animals and to track their movements, all study lions were fitted with GPS satellite radio-telemetry collars (African Wildlife Tracking, Pretoria, South Africa), programmed to record geographical locations once per hour from 17:00 to 07:00 local time, and at 12:00 and 14:00.

We used surgically implanted (see below) miniature temperature-sensitive bio-loggers (DST centi loggers, Star Oddi, Gardabaer, Iceland) covered in inert surgical wax (Sasolwax 1276, SasolWax GmbH, Worthdamm 13-27, D-20457, Hamburg, Germany), programmed to measure T_b at five minute intervals. The miniature temperature bio-loggers (hereafter referred to as temperature bio-loggers) had a measurement resolution of 0.03 °C and range of 5 – 45 °C. We used a high accuracy thermometer (Quat 100, Heraeus, Hanau, Germany) to calibrate temperature bio-loggers in an insulated water bath

at temperatures ranging from 30 - 42 °C. Temperature bio-loggers were calibrated at both the start and end of the study; there was no evidence of calibration drift over time, and bio-loggers were accurate to 0.1 °C post calibration. Data were retrieved by recovering the temperature bio-loggers and downloading the stored temperature data.

We recorded lion activity and acoustic data using custom-built accelerometer bio-loggers (Biotrack/University of Oxford, accelerometer data recorded at 16 Hz, 3 dimensions) and acoustic-accelerometer bio-loggers (Biotrack/University of Oxford, acoustic data recorded at 8 bit, 16 kHz mono, and accelerometer data at 16 Hz, 3 dimensions). The acoustic-accelerometer and accelerometer bio-logger components were covered in dental acrylic for protection, and the bio-loggers were mounted on curved copper plates and bolted to GPS collars. Both acoustic-accelerometer and accelerometer bio-loggers were identical in shape and size, approximately 50 x 20 x 30 mm, and weighed < 150 g. Acoustic-accelerometer bio-loggers recorded audio and accelerometer data simultaneously from the time the bio-logger was turned on (at the time of capture) until the device terminated due to battery failure (approximately one week later). Accelerometer bio-loggers recorded accelerometer data in the same way as acoustic-accelerometer bio-loggers, from the time of capture until battery failure, but did not include an audio component and so recorded accelerometer data for longer periods (three to six months).

Audio and accelerometer data were stored on a standard micro SD card and the data were obtained by recovering the bio-logger and extracting the micro SD card.

3.5. Study animals

Between February 2010 and February 2015, 31 lions (14 female, 17 male) in BVC were captured and fitted with GPS satellite radio-telemetry collars (African Wildlife Tracking, Pretoria, South Africa) and monitored regularly as part of a long term research project. The GPS satellite collars were used to regularly find and observe the study animals (weekly – monthly). When the animals were observed we made field notes of their behaviour, body condition, apparent territorial status, and recorded other lions present with the collared study animal.

In January 2014, we re-captured and fitted 18 of these study lions (six female, 12 male) with temperature bio-loggers. All females were mature adults that had previously suckled cubs, and ranged in age from five to nine years. Males included one sub-adult (defined as younger than four years old) and 11 adults, and ranged in age from 3.5 to 10 years old. We simultaneously fitted accelerometer bio-loggers to 10 of the study animals (three female, seven male) that received temperature loggers. During the study, in November 2014, we re-captured eight of the study lions (three female, five male), removed their accelerometer bio-loggers if they had been previously fitted with one, and fitted the lions with acoustic-accelerometer bio-loggers. A summary of the individuals used in this study and the various bio-loggers that they were fitted with is included in (supplementary data table S.2).

We recovered 840 days of accelerometer data (range 20-146 days per lion, mean 84 ± 48 days per lion), from the 10 study animals that were fitted with both temperature bio-loggers and accelerometer bio-loggers. We recovered a total of 60 days of simultaneous audio and accelerometer data from the acoustic-accelerometer bio-loggers (mean 7.5 ± 2.4 days per lion).

3.6. Capture procedure and mane measurements

Lions were approached by vehicle and darted from a distance of 10 – 35m, with 1cc darts (Type P, $\frac{3}{4}$ " needle with gel collar, Pneudart, Williamsport, Pennsylvania, USA), loaded with a tiletamine:zolazepam combination (Zoletil, 75-100mg, 250mg/ml, Virbac RSA (Pty) Ltd, Halfway House, South Africa) and medetomidine (5mg, 50mg/ml, Kyron Laboratories, Johannesburg, South Africa). Darts were delivered by a CO2-pressurized dartgun (Dan-Inject, Børkop, Denmark). Once the animal appeared to be immobilised (12-15 minutes later) it was approached carefully and a blindfold was placed over the eyes. The front legs were secured with a rope, and earplugs inserted to dampen auditory stimuli.

While lions were immobilised for bio-logger fitting, we took measurements of mane length for male lions; at the crest of skull, crest of shoulder, point of jaw, and centre of chest. The various mane length measurements were then summed to give a total length score that was used as a proxy for mane

length. We also classified each lion mane according to colour as dark, medium, or light, based on a visual assessment of the mane colour.

After bio-loggers had been fitted, the effects of medetomidine were reversed with atipamezole (Antisedan 5mg/ml, Pfizer Animal Health, Johannesburg, South Africa) at a dose of 2.5 - 5 times the total medetomidine dose. We administered half the atipamezole intramuscularly and the other half intravenously. Lions took between 15 and 90 minutes from the time of antidote administration to recover sufficiently from the drug effects in order to be able to walk, but were monitored for a minimum of 3 hours post capture.

3.7. Surgical procedure

Using sterile surgical procedures, temperature bio-loggers were implanted between the parietal peritoneum and the transversus abdominis muscle via an incision in the paralumbar fossa. The loggers were dry-sterilized in formaldehyde vapour before implantation. After administering a local anaesthetic (5 ml 2 % lignocaine hydrochloride, Bayer Animal Health (Pty) Ltd. Isando, South Africa) subcutaneously, we shaved the surgical site, and sterilized it with 5 % chlorhexidine gluconate (Hibitane, Astra Zeneca, Johannesburg, South Africa) in 100 % ethanol. Temperature loggers were tethered to the abdominal muscle wall with nylon (0 USP, Scimitar Surgical Sutures, Gabler Medical (Pty) Ltd, Cape Town, South Africa) to ensure they maintained their original position. Once the loggers were implanted, the incision was sutured closed with absorbable suture material (Viamac, Scimitar Surgical Sutures, Glaber Medical (Pty) Ltd, Cape Town, South Africa) and then treated with a topical antiseptic spray (Necrospray, Centaur Labs, Johannesburg, South Africa) and covered with tick grease (chlorfenvinphos 0.3 %, Swavet Tick Grease, Swavet RSA (Pty) Ltd.). The lions received a long-acting antibiotic (6000 IU/kg of intramuscular procaine benzylpenicillin, Duplocillin, Intervet, South Africa) and a non-steroidal anti-inflammatory analgesic (0.2 mg kg⁻¹ of subcutaneous meloxicam, Metacam, Boehringer Ingelheim, Johannesburg, South Africa).

Post-surgery the lions were observed for several hours until it was determined to be safe by a veterinarian to leave the animal unattended. All animals were checked on opportunistically in the ten

days following surgery and intermittently thereafter. No problems were observed with the recovery and all lions returned to their social groups within a few hours of the surgical procedure.

3.8. Data analysis

3.8.1. Determining feeding

To determine when lions did, and did not feed, we used accelerometer data from the accelerometer bio-loggers. Accelerometer data was classified to infer lion behaviour as either feeding or non-feeding, using machine learning techniques trained with labelled data from acoustic-accelerometer bio-loggers.

We summarised the raw accelerometer data, from both accelerometer and acoustic-accelerometer bio-loggers, into 5 minute periods associated with 12 descriptive feature parameters (mean acceleration and mean variance of acceleration in the X, Y, and Z dimensions; mean and variance of Overall Dynamic Body Action (ODBA); and the mean and variance of the pitch and roll of the bio-logger). We constructed a large data set of labelled accelerometer data from the acoustic-accelerometer bio-loggers by listening to play backs of all the audio data and labelling the simultaneously collected accelerometer data, as either feeding, or non-feeding behaviour. Feeding behaviour could be determined by growls, chewing, and bone crunching sounds. From the audio dataset we labelled 47 h of recorded feeding behaviour, and 769 h of non-feeding behaviour. The labelled accelerometer data was re-organised into a random order then classified using a random forest method (Breiman, 2001), with 1000 trees and four variables per split. The classification model achieved an out-of-bag (OOB) estimated error rate of 1.7 %. Feeding was misclassified as non-feeding behaviour at an error rate of 22.2 %, and non-feeding behaviour was classified as feeding at a class error rate of 0.4 %.

After examining the predicted classification against the known behaviour we discovered that the majority of the false positive classification errors (non-feeding behaviour classified as feeding) were characterised by single isolated feeding events. We then added a second classification layer that removed single isolated feeding events and compared our remaining predicted behaviour against the

entire labelled dataset. Although we generally underestimated the amount of time spent feeding (error rate for feeding classified as non-feeding was 22.2%), all feeding events (44) in the 60 days of recorded lion behaviour were detected (table 1), and no false feeding events were inferred. We then used the random forest model, and second classification layer, to classify the accelerometer obtained from accelerometer bio-loggers.

The classified data from the accelerometer bio-loggers was used to determine whether or not lions with temperature loggers fed on a particular day (binary variable referred to as “feed day”), and if lions did feed on a particular day, we used the time spent feeding (the number of five minute periods classified as feeding, divided by 12 to convert to hours) as a proxy for meal size.

3.8.2. Determining water intake

To test whether males may compensate for a thermal cost of a mane through evaporative heat loss we attempted to assess whether male lions drank more than females during individual drinking events, and whether male lions drank more frequently than females. To determine whether male lions drank more than females during drinking events, we manually listened to the audio data recovered from the acoustic-accelerometer bio-loggers for the sounds of lions drinking. We attempted to quantify the time spent drinking and the “lap rate” during drinking, for individual drinking events. Prior to this we excluded days during which the audio data was not of sufficient quality for us to be confident in determining drinking (feeding behaviour is loud and audible even on lower quality recordings). After removing days during which audio data was not of good quality, we remained with 49.7 days of clear audio data from seven study lions (three female, four male, all resident individuals), during which drinking events (characterised by gentle, consistent lapping sounds lasting between two and 14 minutes, interspersed with a “swallow” sound approximately every 30 seconds), were clearly audible. The individual lions included in the analysis as well as the audio data recovered from the acoustic-accelerometer bio-loggers are summarised in table 1.

When lions were determined to be drinking we recorded the exact start and stop times, by pausing and playing back if necessary, in the software program Audacity 2.1.1. In this way the time

duration measurements of drinking events were accurate to about 1 second. Occasionally lions drank for several minutes, paused for a break (lasting several seconds to several minutes) and then continued drinking. We considered these instances to be drinking bouts that were part of the same drinking event, paused the timer during breaks in the drinking, and summed the individual drinking bouts to determine the total time spent drinking.

We also measured the mean “lap rate” during drinking for each individual, by counting the number of audible “laps” made in one minute time periods of continuous drinking for each lion. One minute periods were taken from at least three separate drinking events for each of the seven lions for which we had clear audio data.

We could not use the audio data to determine the frequency of drinking because the data set spanned too short a time period to quantify differences in drinking frequency between males and females, and because the removal of days when audio data was not clear meant that the audio data was not continuous over that period. Instead, we used GPS data from the lions’ collars to compare the frequency of visits to water points by resident and nomadic, male and female lions on BVC. Only collar data collected between the beginning of June and the end of August, of each year between 2010 and 2014, were included in the analysis, because this period represents the late dry season at the study site, when surface water is only available at known locations. We included as many collared lions as possible and did not restrict the analysis to those lions that had been fitted with temperature bio-loggers. We did however, restrict the analysis of collar data to lions that had at least 80 days of continuous collar data available for that period (females 1784 days of collar data from 13 lions, males 1710 days of collar data from 13 lions; supplementary data table S.3).

All available surface water was accurately marked using a hand held GPS (Garmin, etrex 10, USA). Analysis was carried out in ARCGIS 10.1. Surface water point locations were added as a GIS layer, and a 75 m buffer (the approximate area of a water point and surrounding piosphere) was added around each point. Visits to water points were inferred from lion movement trajectories that

intersected with water point locations. For each lion we calculated the frequency of visits to water per day by dividing the number of visits to water, by the number of days for which collar data was available.

3.9. Statistical analyses

All statistical analyses were carried out using the software program R (R Core Team, 2015). We calculated 24 h summary statistics of mean, minimum, maximum and amplitude (difference between 24 h maximum and minimum) T_b for each 24 h period for each individual. As lions are nocturnal, the 24 h period was taken from 12:00 (midday local time) to 11:59 the next day, to capture activity bouts in single time periods. Female T_b during pregnancy (three females experienced pregnancy) was excluded because we observed different thermal patterns of T_b in pregnant females (Trethowan et al., *in preparation*). Female T_b during lactation was not different to that in non-lactating females (Trethowan et al., *in preparation*), and was thus included in the analysis. When we analysed the effects of sex and mane characteristics on T_b , we summarised T_b parameters for each individual in each meteorological season from the 24 h summary periods. When assessing the relationship between feeding and T_b we used the 24 h summaries for each individual without summarising by season. We also calculated the mean absolute maximum T_b of males and females.

The absolute recorded maximum T_b of males and females was compared using a student's t-test. We used package *nlme* (Pinheiro et al., 2011) to perform linear mixed effects analysis of various fixed effects (see below) on T_b . The best performing model was then selected based on Akaike Information Criterion corrected for small sample size (AICc) using the R package *MuMin* (Barton, 2015). We did not use model averaging which generates misleading unreliable estimates where predictor variables are correlated (Cade, 2015).

We conducted a linear mixed effects analysis of the relationship between T_b , and season and sex. For both seasonal 24 h maximum T_b and seasonal 24 h mean T_b , we tested multiple *a-priori* candidate models (supplementary data table S.4) with season and sex as fixed effects and a possible interaction between them. Individuals were included as a random intercept in all models. We also carried out a linear mixed effects analysis to investigate the relationship between "feed day" (whether

or not the lion fed on a particular day), sex, black globe temperature, and T_b (supplementary data table S.5). We included 24 h maximum black globe temperature, sex, and the binary categorical variable feed day, as fixed effects. As dependant variables we used 24 h maximum T_b in the first analysis, and 24 h mean T_b in subsequent analysis. Individuals were included as random intercepts in all models. Males and females might have different T_b responses to feeding or black globe temperature so we included interaction effects between these terms, and because there was likely to be temporal auto-correlation, we included an autoregressive correlation structure of order one.

We used a linear mixed effects analysis to determine the relationship between mane size and colour on 24 h mean and 24 h maximum T_b . Our dependent variables were seasonal 24 h maximum T_b in the first analysis, and seasonal 24 h mean T_b , in subsequent analysis. Season, mane length, and mane colour were included as fixed effects and individuals were included as random effects (supplementary data table S.6).

The duration, lap rate and total number of laps, during male and female drinking events, were compared using linear models, with sex as the explanatory variable. Individuals were included as a random effect because multiple measurements were taken for each individual. A P-value was obtained with a Satterthwaite approximation (Kuznetsova et al., 2015). We used the same method to compare the frequency of visits to water points where the same individuals were measured in different years; a linear mixed effects models with the individual included as a random effect, and sex and territorial status as fixed effects. An interaction term was included between the effects of sex and territorial status to test for the possibility that the effect of sex depended on territorial status.

4. Results

4.1. Weather

As is typical of the study area, weather conditions were generally hot and dry. Dry bulb air temperature ranged from an absolute minimum of -0.5 °C recorded in winter to a maximum of 46.1 °C recorded in spring, and black globe temperature ranged from -1.6 °C to 61.9 °C, in the same respective seasons. Lions were routinely exposed to high temperatures. Maximum dry bulb air temperature

exceeded 38.0 °C on 39 days during the study and maximum black globe temperature exceeded 38.0 °C on 276 days during the study. A complete summary of the weather parameters per season is given in supplementary data table S.1.

4.2. Effect of sex and season on T_b

Analysis of 24 h maximum T_b revealed that the best performing model included an effect of season ($F_{3,43} = 4.4$, $p = 0.009$) but not sex, a closer inspection of the second best performing model revealed that sex did not have a significant effect on 24 h maximum T_b ($F_{1,16} = 2.4$, $p = 0.1$). However, analysis of 24 h mean T_b , included a relationship between both sex ($F_{1,16} = 6.6$, $p = 0.02$) and season ($F_{3,43} = 11.5$, $p < 0.001$) on 24 h mean T_b , which was an average of 0.2 ± 0.1 °C lower in males than in females across seasons. There was no difference ($t(16) = 1.0$, $p = 0.4$) in the absolute maximum recorded T_b of males (41.0 ± 0.5 °C) and females (40.8 ± 0.3 °C). Mean seasonal parameters of T_b for males and females are summarised in table 2.

4.3. Body temperature on days when lions did and did not feed

The best performing model predicting 24 h maximum T_b included effects of both feed day ($F_{1,824} = 18.0$, $p < 0.001$) and sex ($F_{1,8} = 10.0$, $p = 0.01$), but no effect of 24 h maximum globe temperature or interaction effects. On days when lions fed, 24 h maximum T_b was an average of 0.2 ± 0.1 °C higher than on days when they did not feed. After correcting for feeding, 24 h maximum T_b of males was an average of 0.3 ± 0.1 °C lower than females.

Feed day ($F_{1,822} = 43.0$, $p < 0.001$), sex ($F_{1,8} = 6.5$, $p = 0.03$), and 24 h mean black globe temperature ($F_{1,822} = 19.4$, $p < 0.001$) had an effect on 24 h mean T_b . On days when lions fed, 24 h mean T_b was an average of 0.2 ± 0.0 °C higher than on days when they did not feed (table 3). After correcting for the effects of feeding and black globe temperature, males had a 24 h mean T_b that was 0.8 ± 0.2 °C lower than females. There was an interaction between feed day and sex ($F_{1,822} = 8.1$, $p = 0.005$), with 24 h mean T_b increasing more in males than females on days when they fed. However, this difference was small (female T_b increased by 0.17 °C compared to male T_b by 0.18 °C on feed days), and likely to

be of no biological importance. Twenty four hour mean and 24 h maximum T_b on days when lions did and did not feed is summarised for males and females in table 3.

4.4. Mane length and colour

As shown by our study animals, male lions on BVC develop prominent manes and display a range of mane lengths and colours (table 4 and figure 1). The best performing model predicting 24 h maximum T_b did not include an effect of mane length or mane colour (figure 2a and 2c). However, there was a relationship between both mane length ($F_{1,7} = 5.8$, $p = 0.05$; figure 2b) and mane colour ($F_{2,7} = 6.4$, $p < 0.03$; figure 2d) on 24 h mean T_b . After correcting for season, there was a 0.1°C decrease in 24 h mean T_b for each 100 mm increase in total mane length (figure 2b). The relationship between 24 h mean T_b and mane colour was not as linear as might have been predicted; medium-coloured manes were associated with the highest 24 h mean T_b (figure 2d). Light-coloured manes were associated with a 24 h mean T_b that was about $0.3 \pm 0.1^\circ\text{C}$ lower than medium-coloured manes, and dark manes were associated with a 24 h mean T_b that was $0.1 \pm 0.1^\circ\text{C}$ lower than medium-coloured manes.

4.5. Frequency and duration of drinking

Male lions drank for longer (374 ± 113 seconds) than females (184 ± 84 seconds) during drinking episodes recorded on the acoustic-accelerometer data loggers ($F_{1,5} = 5.9$, $p = 0.06$; figure 3a). Sex affected lap rate ($F_{1,5} = 22.1$, $p = 0.005$), with male lap rates (1.5 ± 0.06 laps s^{-1}) being about 0.4 laps s^{-1} slower than female lap rates (1.9 ± 0.04 laps s^{-1} ; figure 3b). Consequently there was no significant difference in the total number of laps per drinking episodes between males and females ($F_{1,5} = 2.3$, $p = 0.2$), though the mean number of laps was higher for males than females (figure 3c). There was strong evidence that the effect of sex, on the frequency of visits to water, depended on territorial status ($F_{1,11} = 19.7$, $p < 0.001$). Resident male lions visited water points more than twice as often as females or nomadic males (figure 3d), and there was no difference in the frequency of visits to water points between nomadic males and females ($F_{1,24} = 0.3$, $p = 0.8$), or dominant females and nomadic males and females ($F_{1,11} = 0.4$, $p < 0.7$).

5. Discussion

To determine whether there may be a thermal cost to male lions in possessing a mane, we investigated the thermal biology of the lion by measuring T_b continuously for approximately one year in 18 free-living lions, the largest cohort of free-living large mammals for which T_b has been recorded over an extended period of time. Our study was carried out in a hot semi-arid environment where day-time temperatures frequently exceed T_b , and where lions are known to develop prominent manes. Despite the hot conditions and the large, dark manes of some of the study animals, male lions had a 24 h mean T_b that was about 0.2 °C lower than that in females, and there was no difference between male and female 24 h maximum T_b . In addition, between males, both mane colour and length did not influence 24 h maximum T_b , and 24 h mean T_b was negatively correlated with mane length. Thus, our results, derived from the first measurements of T_b in free-living lions, do not suggest that the presence and form of the mane are associated with a thermal cost.

Lions are capable of making efficient use of moisture derived from their prey (Owens and Owens, 1984, Eloff, 1973), so feeding also will provide a water source to support evaporative cooling and regulation of T_b in hot conditions. Because male lions did not have higher T_b than female lions, it seems unlikely that male lions would need to reduce their feed intake during hot periods to avoid increased heat loads, as inferred by the observation that male lions had smaller bellies than did females in hot months (West and Packer, 2002). Postprandial specific dynamic action, the cost of digesting food and the associated increase in metabolic activity, is well documented in the literature and known to increase T_b in some species (Secor, 2009). In cheetah however, the only other free-living felid in which T_b has been measured, an increase in T_b after hunting was associated stress hyperthermia and not feeding (Hetem et al., 2013). Our data do not support the idea that male lions need to reduce food intake during hot conditions. On days when lions fed, both sexes had higher 24 h mean and 24 h maximum T_b than on days during which they did not feed and the increase in temperature with feeding was lower for males than for females. We did not attempt to determine whether elevated T_b was caused by activity (hunting), specific dynamic action, or stress hyperthermia (as likely in the case of

cheetah; (Hetem et al., 2013)), as we were interested in whether males needed to reduce food intake as a consequence of higher T_b . We believe it is unlikely, therefore, that smaller belly sizes observed in male lions in hot months reflect reduced feeding associated with regulating T_b . Less distended bellies in males in hot months could result from a variety of factors. For example, in hot months lions may require less food intake and dominant males with territories to defend (and their associated large manes) may devote more time to territorial defence than feeding.

Our results, that male lions with long dark manes did not have higher T_b than females or males with smaller manes, can be explained in one of two ways; either there is no thermal cost to lions in possessing a mane, or a thermal cost to the mane does exist, but males compensate for the increased heat burden with increased heat loss. It seems intuitively obvious that a thick dark mane in a hot African savannah would be associated with a thermal cost as it may facilitate heat gain and impair heat loss. However, a darker and longer mane will not necessarily result in greater heat gain by the animal. Although a darker colouration may absorb more short-wave radiation from the sun, the structure and density of hairs on an animals' pelt influences the depth to which heat penetrates the pelt (Walsberg, 1983). In lions, the dark mane hairs are thicker than those of light mane hairs (West and Packer, 2002), which may act to increase the insulation of the pelt. A highly insulated pelt may create a "heat shield" that allows some of the radiant heat absorbed near the surface of a pelt to be dissipated back into the environment through conduction, convection, and radiation (Tattersall et al., 2012). For example, merino sheep in the unshaded desert planes of Australia, had surface temperatures as high as 87 °C, but a remarkable 45 °C temperature gradient was sustained between the tip of the wool and the skin, by the 40 mm thick pelage (Macfarlane et al., 1956). In the case of a heat shield, pelt thickness and black (or dark) colouration can be beneficial (Tattersall et al., 2012). It is possible, therefore, that a long dark mane may allow males to remain in the sun for longer than for males with a short or light-coloured mane. Increased insulation by the mane may explain the weak but significant negative correlation we detected between mane length and 24 h mean T_b , and why lions with dark manes had cooler 24 h mean T_b than those with medium-coloured manes. Nocturnal activity combined with shade-seeking during

the day by inactive lions (Schaller, 1972) also will further reduce the influence of mane colour on radiant heat gain by lions.

Increased insulation in the neck and chest region is unlikely to impair the ability of male lions to lose heat at high ambient temperatures (similar to or above T_b). When environmental temperatures exceed T_b , as occurs frequently in savannah habitats occupied by lions, and in our study, heat can be dissipated only by evaporation. Domestic cats rely on panting for evaporative heat loss (Adams et al., 1970). They do not possess functional sweat glands over the body and, contrary to a widely held view, sweat glands found on their paws (Munger and Brusilow, 1961) do not contribute to regulating heat balance (Adams et al., 1970). Like other cats, lions probably do not sweat across their fur and primarily rely on evaporative cooling during panting and licking of their fur, which is not impaired by the presence of the mane. When ambient temperatures are lower than T_b , lions lose heat by rolling on their backs and exposing their thin-skinned loins (Smith and Kok, 2006), which are not covered by the mane and may act as a thermal window. It is unlikely, therefore, that the mane impairs heat loss, particularly at high environmental temperatures when evaporative cooling is obligatory.

Although we have demonstrated that a darker and longer mane does not increase T_b , it could be argued that males increase heat loss to compensate for a thermal cost of the mane. Such compensatory behaviour would likely necessitate increased water intake, particularly for lions, like ours, in hot environments. The estimated required evaporation for thermoregulation decays exponentially in relation to body size (Schmidt-Nielsen, 1997). Consequently, for a large sexually dimorphic mammal such as a lion, where males and females have different body masses (average female 126 kg, male 190 kg; Skinner and Chimimba), both sexes require about the same percentage of body mass (about 1.25 % of body mass in the case of lions), for evaporation. Thus males are expected to require about 50 % more water for evaporative heat loss than are females.

Male lions did not drink more than females in terms of the total number of laps per drink episode, though male lions are larger than females, and their bigger mouths may allow them to ingest more water than females per lap; possibly making up the 50 % extra water they require on account of

their body size. However, we found that resident territorial male lions visited water points more than twice as frequently as did females or nomadic males, and this finding strongly suggests that water points are considered an important resource by resident (dominant) males. Dominant pride males are known to have longer, darker manes than nomadic males (West and Packer, 2002), and may visit water more frequently than nomadic males to increase water uptake and offset the thermal cost of their large dark manes. In such cases, male lions with long dark manes would be signalling access to drinking water rather than greater tolerance of higher thermal loads, as was previously suggested (West and Packer, 2002). However, dominant male lions might frequent water points more than females for reasons other than a need to drink. For instance, water points are typically surrounded by an open piosphere (Washington-Allen et al., 2004) that may constitute a good place for lions to roar because sound travels further. Water points may also provide definite locations in the landscape for territorial scent marking, which males might use more than females. Finally, water flux rates may also differ between males and females for reasons other than thermoregulation, such as higher rates of “spraying” by males during territorial scent marking, necessitating increased water uptake by males for reasons other than increased evaporative heat loss. Thus the question of whether male lions increase evaporative heat loss to compensate for the thermal properties of the mane remains inconclusive, but it is clear that maned lions with access to water do not have higher T_b than females, or than males with shorter manes.

6. Acknowledgements

We would like to thank the shareholders of Buby Valley Conservancy for allowing us to conduct field research on the conservancy. We would also like to thank the management staff of Buby Valley Conservancy for assistance in the field. Paul Trethowan would like to thank Dr Paul Johnson for statistical advice.

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8. Tables

Table 1. Summary of total audio data collected per lion (days), clear audio data remaining after removing low quality recordings (days), and the number of feeding events, and drinking events recorded.

ID	Sex	Total audio	Clear audio	Feed	Drink
Lion 7	Male	6.8	0	3	0
Lion 8	Male	10.9	10.9	5	11
Lion 13	Male	11	8.8	5	16
Lion 14	Male	8.8	5.2	5	5
Lion 16	Male	3.2	3.2	2	4
Lioness 4	Female	7.1	4.4	7	4
Lioness 7	Female	8.9	8.8	8	13
Lioness 14	Female	8.9	8.4	9	11

Table 2. Mean and standard deviation of T_b parameters for males (M) and females (F) in each season. N denotes the number of individuals.

T_b (°C)	Season							
	Dec - Feb 'Summer'		Mar - May 'Autumn'		Jun - Aug 'Winter'		Sep - Nov 'Spring'	
	M (n=12)	F (n=6)	M (n=12)	F (n=6)	M (n=10)	F (n=5)	M (n=8)	F (n=5)
Mean	37.7 ± 0.1	37.8 ± 0.1	37.5 ± 0.2	37.7 ± 0.1	37.3 ± 0.3	37.5 ± 0.5	37.5 ± 0.2	37.7 ± 0.1
Minimum	36.7 ± 0.2	36.7 ± 0.3	36.3 ± 0.2	36.8 ± 0.2	35.9 ± 0.4	36.3 ± 0.5	36.0 ± 0.3	36.4 ± 0.3
Maximum	38.8 ± 0.1	39.0 ± 0.1	38.7 ± 0.2	38.8 ± 0.1	38.6 ± 0.4	38.6 ± 0.6	38.8 ± 0.2	39.0 ± 0.1
Amplitude	2.1 ± 0.2	2.3 ± 0.3	2.5 ± 0.3	2.1 ± 0.2	2.7 ± 0.6	2.3 ± 0.3	2.8 ± 0.5	2.6 ± 0.3

Table 3. The 24 h maximum and 24 h mean T_b for males and females on days with and without feeding. Data are shown as the mean with standard deviation between individuals. Number of individuals indicated in parenthesis.

Sex		24 h mean T_b (°C)		24 h maximum T_b (°C)	
		No feed	Feed	No feed	Feed
	Male (n = 10)	37.4 ± 0.1	37.8 ± 0.2	38.3 ± 0.2	38.8 ± 0.2
	Female (n = 3)	37.6 ± 0.2	37.9 ± 0.2	38.5 ± 0.4	39.1 ± 0.3

887 Table 4. Lion mane measurements (mm), length score, and colour class.

ID	Mane measurements				Length score	Colour class
	Skull	Shoulder	Jaw	Chest		
Lion2	100	200	100	180	580	Dark
Lion3	140	50	90	200	480	Light
Lion5	190	190	90	210	680	Dark
Lion6	120	160	100	220	600	Medium
Lion7	160	170	90	200	620	Light
Lion8	190	190	80	200	660	Medium
Lion9	60	180	90	230	550	Medium
Lion12	80	160	80	230	550	Medium
Lion13	150	150	100	240	640	Dark
Lion14	100	200	100	250	650	Medium
Lion16	180	130	90	220	610	Dark
Lion17*	-	-	-	-	-	Light

888 *no reliable mane measurement was recorded for Lion17.

889 9. Figure legends

890 Figure 1. Photographs of all 12 male lions included in this study. L, lion ID.

891 Figure 2. The 24 h maximum and mean T_b of male lions by mane colour class and length score a) Shows
892 the 24 h maximum T_b ($^{\circ}\text{C}$) for each male lion and b) the 24 h mean T_b for each male lion, against mane
893 length score (mm), c) shows the mean 24 h maximum T_b between individuals and d) the mean 24 h
894 mean T_b between individuals, against mane colour category from light to dark. For mane colour, n
895 indicates the number of individuals; the mean is calculated between individuals. Error bars indicated
896 one standard deviation from the mean.

897 Figure 3. Drinking behaviour and frequency of visits to water points in lions a) The mean duration of
898 male and female drinking episodes (seconds). b) The mean lap rate (laps per second) during drinking
899 for males and females. c) Mean number of total laps for males and females during drinking episodes.
900 d) Mean number of visits to water points per day by sex and territorial status (NF = nomadic female,
901 NM = nomadic male, RF = resident female, RM = resident male). Means calculated between individuals.
902 Error bars show standard deviation from the mean. N shows the number of individuals.