Keeping cool in the heat: Behavioral thermoregulation and body temperature patterns in wild vervet monkeys

Running title: *Keeping cool in the heat*

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Abstract

Objectives: Climate change is having a significant impact on biodiversity and increasing attention is therefore being devoted to identifying the behavioral strategies that a species uses to cope with climatic stress. We explore how wild vervet monkeys (*Chlorocebus pygerythrus*) respond to heat stress, and how behavioral adaptations are used to regulate body temperature.

Materials and methods: We implanted wild vervet monkeys with temperature-sensitive data loggers and related the body temperature rhythms of these animals to their use of thermoregulatory behaviors.

Results: Environmental temperature had a positive effect on the mean, minima and maxima of daily body temperatures. Environmental temperature had a positive effect on the amount of time that vervet monkeys spent in the shade, and animals that spent more time in the shade had lower body temperature maxima. Drinking water did not have a proximate effect on body temperature, most likely a consequence of their regular access to drinking water. Body temperatures were observed to decrease after swimming events, but tended to return to pre-swim temperatures within one hour, suggesting a limited thermal benefit of this behavior.

Conclusions: Our data support the view that vervet monkeys cope well in the heat, and use behavior as a means to aid thermoregulation. The ability of primates to be flexible in their use of thermoregulatory behaviors can contribute positively to their capacity to cope with environmental variability. However, given its broad effect on plant productivity and habitat loss, climate change is a major threat to species' biogeographical distribution and survival.

Key words: Behavior; Body temperature; Climate; Thermoregulation

Introduction

Climate change is exerting a significant impact on biodiversity (Cahill et al., 2013; Pacifici et al., 2015; Scheffers et al., 2016; Urban et al., 2016) and, consequently, greater attention is being paid to the strategies that may allow different species to cope with climatic stress. Due to the long generation time of mammals it is expected that genetic adaptation will not be an effective response to climate change, and that species survival will be dependent on both physiological and behavioral flexibility (Fuller et al., 2010). Behavioral flexibility refers to transient changes in the behavior of an individual in response to changes in their environment (Kappeler et al., 2013; Strier, 2017). Behavioral flexibility has consistently been argued to be adaptive in its ability to buffer an individual or species from the effects of climate change (Parmesan, 2006; Fuller et al., 2010; Hetem et al., 2014; McFarland et al. 2014). Empirical evidence in support of this claim, however, is scarce, given the necessity to collect data from free-living animals over long time periods (Porter et al., 2008; Kearney et al., 2009; Seebacher & Franklin, 2012; Hetem et al., 2014; Campos et al., 2017). Nevertheless, furthering our understanding of how present-day populations express behavioral flexibility in response to environmental variability, especially in extreme climates, remains an important focus of research. Understanding how a species responds to climatic stress, and the degree to which behavior can be used to buffer an individual from thermal stress, provides important insights in to how a species might adjust to new environments. For example, the behavioral response of an animal to thermal stress is an important component of model simulations that predict how a species will fare in the face of climate change (Carey, 2005; Porter et al., 2008; Kearney et al., 2009; Korstjens et al., 2010; Lehmann, Korstjens & Dunbar, 2010; Mathewson, 2018).

For primates, most previous studies have focused on the behavioral correlates of environmental variability (e.g., resting, foraging and social activity: Hill, 2006; Campos & Fedigan, 2009; Korstjens, Lehmann, & Dunbar, 2010; Majolo, McFarland, Young & Qarro, 2013; McFarland, Barrett, Boner, Freeman & Henzi, 2014), with less attention devoted to the physiological processes that underpin these relationships. While these studies provide important insights into the relationship between environmental and behavioral variables, they offer little on the consequences of environmental variability for a primate's physiology, its ability to thermoregulate, or the effectiveness of particular behaviors as buffers against environmental heat or cold. Only a few studies have related thermoregulatory behaviors and activity patterns directly to measures of core body temperature (e.g., Brain & Mitchell, 1999; Schmid, 2000, Schmid, Ruf & Heldmaier, 2000; Dausmann 2005; Lubbe et al., 2014; McFarland et al., 2015; Henzi et al., 2017), while others have tended to use skin or subcutaneous temperature measurements to approximate core body temperature (Dausmann et al. 2004; Nowak et al. 2010, 2013; Blanco et al. 2013; Kobbe et al. 2014; Thompson et al. 2014).

Primates, like all mammals, employ a range of behavioral adjustments to help reduce the autonomic costs of thermoregulation. To maintain homeothermy in cold environments, autonomic responses include an increase in metabolic heat production, and typically feeding time increases to meet this demand (Hill, 2006; Campos & Fedigan, 2009; Majolo et al., 2013; McFarland et al., 2014). In concert with autonomic responses, primates also employ behavioral thermoregulation, such as huddling that reduces heat loss and sun-basking that increases radiant heat gain (Takahashi, 1997; Ogawa & Takahashi, 2003; Danzy, Grobler, Freimer, & Turner, 2012; McFarland et al. 2015; Kelley, Jablonski, Chaplin, Sussman & Kamilar, 2016; Eppley, Watzek, Dausmann, Ganzhorn & Donati, 2017). If energy availability or behavioral mechanisms are insufficient then heat balance is compromised, and changes in the daily pattern of core body temperature become apparent. Primates living in temperate regions are particularly prone to experiencing cold stress (e.g., chacma baboons, *Papio ursinus*: Weingrill, Gray, Barrett & Henzi, 2004; Barbary macaques, *Macaca sylvanus*: McFarland & Majolo, 2013; vervet monkeys: McFarland et al., 2015; Japanese macaques, *Macaca fuscata*: Thompson et al., 2017; Yunnan snub-nosed monkeys, *Rhinopithecus bieti*: Grueter et al., 2009; golden snub-nosed monkeys, *Rhinopithecus roxellana*: Guo et al., 2018). For example, in our study population of vervet monkeys in the Eastern Cape, South Africa, animals exhibited more variable body temperature rhythms in the winter months than they did in the summer months, despite ambient temperatures regularly exceeding 40 °C in summer (McFarland et al., 2013, Lubbe et al., 2014; McFarland et al. 2015, Henzi et al., 2017).

In hot environments, primates employ a suite of behavioral mechanisms that reduce heat load or increase heat loss. Primates will avoid physical exertion and spend more time resting (Hill, 2006; Campos & Fedigan, 2009; Majolo et al., 2013; McFarland et al., 2014), seek out cool microclimates (e.g., shade, caves and existing burrows: Stelzner & Hausfater, 1986; Barrett, Gaynor, Rendall, Mitchell & Henzi, 2004; Hill, 2006; Pruetz, 2007; Duncan & Pillay, 2013; McFarland et al., 2019), or adopt postures that are conducive to heat dissipation (Stelzner & Hausfater, 1986; Bicca-Marques & Calegaro-Marques, 1998; Campos & Fedigan, 2009; Lopes & Bicca-Marques 2017). Indeed, sand basking with cool subsurface sand slowed the daily body temperature rise of chacma baboons in the Namib Desert, Namibia (Brain & Mitchell, 1999). However, behavioral mechanisms that enhance dry-heat loss can be effective only if substrates or environments are cooler than the animal. When environmental temperatures exceed body temperature, then mammals must rely exclusively on evaporative cooling to achieve heat balance

(Mitchell et al., 2018). In primates, evaporative heat loss can be increased via both sweating and panting (Hiley, 1976; Kimani, 1983; Campos & Fedigan, 2009). These autonomic thermoregulatory mechanisms can be sustained only if an endotherm has sufficient access to water (Hetem, Maloney, Fuller & Mitchell, 2016). When exposed to high ambient temperatures with limited access to water, both wild and captive chacma baboons develop severe hyperthermia (Brain & Mitchell, 1999; Mitchell et al., 2009). To date, few studies have attempted to link thermoregulatory behaviors directly to proximate changes in the core body temperatures of a wild primate.

Here, we investigate the use of thermoregulatory behavior by vervet monkeys in response to heat stress, using time-matched body temperature measurements to assess the effectiveness of these behaviors in maintaining homeothermy. Based on our previous findings that vervet monkeys have relatively stable body temperatures in the hot summer months, relative to the winter months (Lubbe et al., 2014), we predicted that vervet monkeys use behavioral adjustments to achieve homeothermy when exposed to heat. Specifically, we tested whether environmental temperatures were related to body temperatures, and how the latter were affected by time spent inactive (resting or allogrooming), in shade, drinking, or swimming. We predicted that vervet monkeys would spend more time inactive (McFarland et al., 2014) in the shade when environmental temperatures were high. Although water availability is highly variable at our study site (McDougall, Forshaw, Barrett & Henzi, 2010), the monkeys had constant access to natural water sources during this particular study period, so we did not expect drinking events to have proximate effects on body temperature like those observed in dehydrated baboons (Brain & Mitchell, 1999). Finally, we did not expect body temperatures to decrease during swimming, as vasoconstriction should prevent a lowering of core body temperatures when exposed to cold for short periods of time. We did, however, predict that body temperatures would decrease following swimming events as a result of an increase in evaporative heat loss from a wet pelage over longer periods of time.

Methods

Data were collected between April 2012 and March 2013 from three groups of wild vervet monkeys in the Eastern Cape, South Africa (32º22’S, 24º52’E). These animals fed on a natural diet, were fully habituated to the presence of researchers, and were individually identifiable by means of natural markings (Pasternak et al., 2013; McFarland et al. 2014). The three groups, RBM, RST and PT, consisted of 47 (17 females, 30 males), 55 (25 females, 30 males) and 26 (12 females, 14 males) adults, respectively. Air temperature was recorded at an onsite weather station every 30 minutes. All statistical summary measures are reported as mean ± SD. Over the 12 months of the study, air temperature ranged from -7 to 43 ºC (mean daily air temperature was 16 ± 6 ºC, with a mean daily maximum of 26 ± 7 ºC and mean daily minimum of 8 ± 5 ºC). Black globe temperature was also recorded at the weather station every 30 minutes. Because the exchange of dry heat between an animal and the environment depends, not only on air temperature, but also on the radiation temperature and the wind speed, the black globe temperature was measured because it incorporates the influence of air temperature, solar radiation, and wind speed. Black globe temperature is thus considered a better measure of the thermal environment than is air temperature alone (Hetem, Maloney, Fuller, Meyer & Mitchell, 2007). The black globe temperature ranged from -4 to 60 ºC (mean daily black globe temperature was 19 ± 7 ºC, with a mean daily maximum of 36 ± 9 ºC and mean daily minimum of 7 ± 6 ºC). Naturally occurring drinking water was available to the animals during the entire study period.

Behavioral data

Instantaneous scan data (Altmann, 1974) were collected daily at 30-minute intervals across all daylight hours, from all adults in groups RBM and RST that could be located within a ten-minute period (totalling 27 098 individual animal scans). Data collection on group PT did not commence until September 2012. Due to limited scan data being collected from PT group across the current study, only groups RBM and RST were the focus of analyses involving scan data. During each scan, all observed subjects were recorded as being either in the sun, in the shade, or under cloud cover (i.e., it was not possible to discriminate between sun and shade). In addition, each subject was recorded as being either active (i.e., foraging or travelling) or inactive (grooming or resting). The scan data were used to calculate a count of males and females in each group that were in the shade and inactive for each hour of each day across the 12-month study period, and the proportion of time each subject spent inactive or in the shade per month. Data were also collected *ad libitum* from data-logged subjects from all three groups. The start and end times of all observed instances of drinking (N = 114) and swimming (N = 9) were recorded, to allow these events to be time-matched to body temperature and black globe temperature measurements.

Swimming behavior among non-human primates serves a range of functions, including expanded range use, aquatic foraging, and possible thermoregulation (Kempf, 2009). Although our vervet monkeys did not forage in the river itself, they live in a semi-arid, riparian woodland habitat (Pasternak et al., 2013), that at times required them to traverse the river (~10 m wide) to reach adjacent parts of their home range. The swimming events analysed in the current study excluded such travelling events, so our predictions could be centered on swimming as a form of behavioral adjustment that may provide thermal benefits.

The behavioral data collection protocols were approved by the University of Lethbridge under Animal Welfare Protocol 0702.

Body temperature data

In April 2012, a subset of 19 adult vervet monkeys (9 females, 10 males) distributed across groups RBM and RST, underwent surgery for the implantation of miniature temperature-sensitive data loggers (model: ADXL345, Sigma Delta Technologies, Perth, Australia) into the peritoneal cavity. The loggers instantaneously recorded core body temperature at five-minute intervals at a resolution of 0.06°C and were individually calibrated to an accuracy of 0.1°C. An additional female and male vervet monkey from group PT were implanted in September 2012 (i.e., after behavioral data collection from this group had commenced). In March 2013, all the data loggers were retrieved. Body mass was recorded for all animals (mean ± SD, female = 3.3 ± 0.4 kg, male = 5.1 ± 1.0 kg). For full details of the capture and surgery procedure see McFarland et al., (2015). Body temperature data were used to calculate the 24 h mean, maxima, minima, and amplitude (i.e., maxima – minima) of vervet monkey body temperature rhythms. All capture and surgical procedures were approved by the University of the Witwatersrand Animal Ethics Research Committee (Protocol # 2010/41/04) and conformed to the legal requirements of South Africa.

Statistical analysis

Model analyses were performed in R (R Core Team, 2017), using the ‘lme4’ package (Bates, Maechler, Bolker & Walker, 2015) to model outcomes, and the MuMIn’ package (Barton & Barton, 2015) to generate marginal and conditional R^2 values for the fixed effect and whole models, respectively (Nakagawa & Schielzeth, 2012). Linear predictor variables were scaled by subtracting the mean from the inputs and dividing the inputs by two standard deviations so that linear and nominal variable coefficients could be directly compared (Gelman, 2008). Prior to running each model, we checked for multicollinearity by calculating Variance Inflation Factors (VIF) for the predictor variables. None of our model variables had a VIF score greater than 6 so were thus retained in their respective models (Kutner, Nachtsheim & Neter, 2004: see for details supporting a VIF criteria of less than 10). All models were compared with the null model (i.e., an intercept only model) using likelihood-ratio Chi^2 tests. The residuals of all final models were normally distributed and thus met the assumptions of normal error structure. We describe outcomes as indicating weak ($P \sim 0.05$), moderate ($P \sim 0.01$) or strong ($P \sim 0.001$) evidence for effects (sensu Colquhoun, 2014).

To test for an effect of environmental temperature on the body temperature rhythms of our subjects equipped with data-loggers, we ran four linear mixed models (LMM) using either 24 h (i) mean, (ii) maxima, (iii) minima, or (iv) amplitude of the daily body temperature rhythm, in turn, as the outcome variable. In all four models, the mean 24 h black globe temperature was entered as a predictor variable. Sex and body mass were also entered as predictor variables to control for potential differences in body temperatures between males and females of variable body mass. Subject ID, nested inside group ID, was entered as a random effect. Analyses were run at the level of the subject-day (N = 3 471 monkey days from 21 monkeys over the 12-month study).

To test the potential effects of environmental temperature on shade-use behavior, we ran a generalised LMM. We specified a negative binomial link function, entering the count (for each sex) of scans in the shade per hour as the outcome variable and the log of the total number of scans as the offset. Mean hourly black globe temperature and subject sex were entered as predictor variables. Day ID, crossed with group ID, was entered as a random effect. Analyses were run at the level of the hour-sex-group (N = 2 514 monkey group hours).

From those subjects equipped with data-loggers, we were able to test for any effect of monthly shade-use behavior on monthly body temperature rhythms. Only subjects that had at least 20 subject scans in a given month were included in these analyses. We ran two LMMs entering either the monthly 24 h body temperature mean, or maxima, in turn as the outcome variable. The mean 24 h black globe temperature, the proportion of time spent in the shade per month, and the proportion of time spent inactive per month, were entered as predictor variables. Subject ID, nested inside group ID, was entered as a random effect. Due to the smaller size of this dataset, we opted to reduce the number of fixed effects in this model by removing subject sex and body mass as predictor variables. Our previous analyses did not reveal significant effects of sex or body mass on vervet monkeys body temperature rhythms (Table 1). Analyses were run at the level of the subject-month (N = 76 monkey months from 15 monkeys over the 12-month study).

We ran three LMMs to test the effect that the act of drinking water had on the body temperature patterns of subjects equipped with data-loggers, over three different time periods. In all three models, time period (i.e., before or after) was entered as the predictor variable. In each of the three models, the following were entered in turn as the outcome variable: (i) body temperature five minutes before and five minutes after the drinking event (i.e., the time resolution of the data loggers), (ii) the average body temperature across a 30-minute period both before and after the drinking event, and, (iii) the average body temperature across a 60-minute period both before and after the drinking event. Drinking duration, subject sex, body mass, and black globe temperature coinciding with the drinking time, were also entered as predictor variables to control for their effects on body temperature. Drinking event ID, nested inside subject ID, nested inside group ID, was entered as a random factor. Analyses were run at the level of the time period/drinking event/subject (N = 278 before and after drinking periods from 139 drinking events from 16 monkeys).

Due to the somewhat limited observation of swimming events by subjects that were equipped with data loggers (N = 9 subjects), body temperature profiles during events are qualitatively described, but were not statistically analysed.

Results

Relationship between environmental temperature and body temperature rhythms

The 24 h body temperature patterns of the vervet monkeys were significantly associated with environmental temperatures (Table 1, Figure 1). There was strong evidence that mean 24 h black globe temperature had a positive effect on the 24 h body temperature means, maxima, and minima, and a negative effect on the amplitude of the 24 h body temperature rhythm. All of the models performed better than their corresponding null models. The model with the mean 24 h body temperature as the outcome variable performed best, with 32 % of its variance explained by the fixed effects, followed by the model of the daily minima (23 %), and amplitude (14 %), and maxima (5 %; Table 1) as the outcome variable.

Relationship between environmental temperature, shade-use, and body temperature

At the group level, the frequency of shade-use per hour was positively associated with environmental temperature (Table 2). There was strong evidence that black globe temperature had a positive effect on the proportion of the group that was in the shade per hour. The model performed better than the corresponding null model (Table 2).

When controlling for the effect of black globe temperature, there was no evidence that either the proportion of time spent inactive per month, or the proportion of time spent in the shade, had an effect on the monthly body temperature means. When controlling for the effect of black globe temperature, however, there was moderate evidence that the proportion of time that was spent in the shade per month had a negative effect on monthly body temperature maxima. There was no evidence that the proportion of time that was spent inactive per month had an effect on monthly body temperature maxima. The models with the body temperature mean and maxima as the outcome variables both performed better than their corresponding null models (Table 3).

Effect of drinking on body temperature

On the occasions when we did observe the vervet monkeys drinking, it was typically in the middle of the day (12:00 ± 2.5h) when the black globe temperature was 32.5 ± 8.8 °C. The mean black globe temperature at 12:00 h across the entire study was 33 °C (mean from 9:00 to 15:00 h: 31 °C). At the time that they commenced drinking, the vervet monkeys had a mean body temperature of 38.6 ± 0.5 °C (N = 114). On average a drinking event lasted 18 ± 10 s. There was no evidence that the act of drinking water effected body temperature in the five minutes immediately after a drinking event (Δ -0.02 ± 0.13 °C), or across a 30-minute (Δ -0.01 ± 0.26 °C), or 60-minute (Δ -0.05 ± 0.35 °C), post-drinking period (Table 4; Figure 2).

Effect of swimming on body temperature

Body temperature data were recorded across nine observed swimming events from four females (Table 5; Figure 3). The body temperature at the start of every swimming event was greater than 38 °C. The body temperature decreased after each swimming episode, and took 63 ± 42 minutes, on average, to reach a minimum after a swimming event (Δ -1.33 ± 0.98 °C), before increasing thereafter. Body temperature returned to the pre-swim levels after 108 ± 55 minutes.

Discussion

Despite the ambient air temperature exceeding 40 °C on some days, the vervet monkeys in this study maintained relatively stable body temperatures, and avoided hyperthermia. The mean daily black globe temperature was positively associated with the 24 h mean body temperature, and negatively associated with the amplitude of the 24 h rhythm of body temperature. Those outcomes were driven predominantly by the positive association between the black globe temperature and the body temperature minima (marginal R^2 = 23%), and, to a lesser extent, its positive association with body temperature maxima (marginal R^2 = 5%). That is, although black globe temperature had a positive effect on both body temperature minima and maxima, it had a stronger effect on the former, meaning the associated body temperature amplitude (i.e., maxima – minima) was smaller in hot conditions. This supports the view that, although cold temperatures are an important stressor for this population (i.e., wider temperature amplitudes in colder conditions: McFarland et al. 2015), body temperature maxima are also sensitive to environmental variability and variable climates. Hyperthermia, and the subsequent risk of heat-related illness in mammals, occurs when body temperature exceeds approximately

42.5 °C (Hiley, 1976; Fuller, Mitchell, Maloney & Hetem, 2016). Chacma baboons in a laboratory, for example, showed signs of heat stroke when body temperature reached 42.5°C (Bouchama et al., 2005). Body temperature in excess of 42.5 °C was never seen in any of our vervet monkeys, and in only 1 % of cases (45 of 4 118 monkey days) did the mean 24 h body temperature exceed 40 °C.

Primates are largely considered to be a tropical or sub-tropical order, given their present-day distribution, and the co-evolution of primates and tropical habitats in the early Eocene (Sussman, 1991; Fleagle & Gilbert, 2006, Smith, Rose & Gingerich, 2006; Sussman, Rasmussen & Raven, 2013). The extant primates are found predominantly in tropical habitats characterised by high temperature, rainfall, and biodiversity. A limited number of primate taxa are found in more temperate climates, characterised by low ambient temperatures, rainfall, and biodiversity (Fleagle & Gilbert, 2006). There are of course exceptions to such a simple climatic delineation between tropical and temperate species. Primate species living in temperate regions can also be exposed to high temperatures and droughts that can potentially result in hyperthermia and heat-related illness. Chacma baboons in the Namib desert, Namibia, for example, were observed to develop hyperthermia when they did not have regular access to drinking water (Brain & Mitchell, 1999). To avoid hyperthermia when environmental temperature exceeds body temperature, an animal must engage evaporative cooling, and to sustain that effector, must be able to replace the water that is lost by evaporative cooling (Fuller et al., 2016; Mitchell et al., 2018). Our vervets had a mean body temperature of 37.8 ± 0.4 °C across the duration of the study. The black globe temperature exceeded 37.8 °C for 12.5 % of the duration of the study. Regular access to drinking water from a river, however, would have made it possible for our vervets to engage in evaporative cooling and replace the water, allowing them to maintain relatively stable body temperatures even during extreme heat (i.e., when ambient temperature exceeded body temperature).

Regular access to water might also explain the absence of a proximate effect of drinking on body temperature. Some previous studies have reported a dramatic decrease in body temperature following a drinking event in primates (Brain & Mitchell, 1999; Mitchell et al., 2009). However, in those studies, the animals were water-deprived prior to the drinking event. When mammals cannot maintain water balance, as might occur when they inhabit an arid habitat, they will gradually become dehydrated. In turn, dehydration leads to an attenuation of evaporative cooling, reducing water use but increasing the likelihood of hyperthermia (Baker, 1989). When the baboons in the studies of Brain & Mitchell, (1999) and Mitchell et al., (2009) were given access to drinking water, they were already hyperthermic, most likely as a result of an attenuation of the evaporative cooling response. When they were given access to drinking water, evaporative cooling was activated, and the body temperature decreased rapidly to a normal (hydrated) level. Our vervets, which likely were well-hydrated, experienced no change in body temperature following a drinking event.

Vervet monkeys likely used autonomic means, especially sweating (Kimani, 1983), to regulate their body temperatures in the heat, but behavioral adjustments may also have played an important role by reducing heat gain and thereby reducing the water costs of evaporative cooling. Coupled with our earlier finding that vervet monkeys in the same study population spent more time inactive when environmental temperatures were high (McFarland et al., 2014), we also found that they spent more time in the shade at high environmental temperatures. Furthermore, this behavioral adjustment was significantly associated with body temperature patterns. We showed that when individuals spent more time in the shade, they had lower body temperature maxima than when they that spent less time in the shade. Overall, our findings confirm the predicted shade-seeking response of vervet monkeys to heat, and that this behavior has a meaningful effect on an individual's thermal physiology.

Although it might seem intuitive that when an animal swims it would provide some cooling benefit while the animal is in contact with water that is cooler than the body (van Schaik, Amerongen & van Noordwijk, 1996; Pruetz & Bertolani, 2009; Kempf, 2009), there will also be an increase in evaporative heat-loss from a wetted pelt in the aftermath of a swimming event. Other mammals, including humans, for example, show no decrease in body temperature during swimming events (Fuller, Oosthuyse, Maloney & Mitchell, 1999; Hidden, 2009). For the first time, notwithstanding the small and descriptive sample, we were able to track the core body temperature patterns of a wild primate before and after swimming events. Vervet monkey body temperatures decreased an average of 1.33 ± 0.98 °C following a swimming event, and the decrease lasted approximately two hours (Table 5). The increase in evaporative heat loss from the wetted pelt likely explains the whole-body cooling observed (wind speed in this environment is on average 3.0 m/s), and would have contributed savings in body-water that would otherwise have been required for sweating, albeit for a relatively short time period.

If swimming were to provide significant thermal benefits, one might expect all of the animals to engage in this behavior. In the current study, while juveniles were frequently observed to swim, the behavior was very rarely observed in adult males, and only occasionally in adult females (hence our small sample size). We implanted only adult monkeys, and so do not have body temperatures from any juveniles. One could argue that the increase in body and muscle mass of adults might offer them some thermal inertia, making them less heat stressed, and therefore less in need of the cooling effects of swimming (Kempf, 2009, but see Mitchell et al., 2018). However, it seems more likely that the higher rates of swimming that were observed among juveniles was probably best regarded as play behavior. While adult females tended to swim for less than a minute, the juveniles swam for extended periods of up to an hour and were often seen engaging in jumping and wrestling behaviors as they engaged with their conspecifics in the water. The more frequent observation of swimming in adult females compared to males might reflect their tendency to stay close to their young offspring during play (Fedigan, 1972). The moderate short-term thermal benefits afforded by swimming in the adults that we monitored, coupled with the hydration and evaporative sweating benefits afforded by regular access to drinking water, makes play the most likely explanation for the relatively infrequent occurrence of swimming among adults during the study period. Importantly, although swimming may have the potential to provide thermal benefits, due to the risks of predation (Cheney et al., 2004; Kempf, 2009) and water-borne diseases (Rideout et al., 1997; Setchell et al., 2007) associated with exposure to open water sources, such opportunities are likely to be restricted to certain populations. Our vervet population is not exposed to aquatic predators, which might explain the tendency of our population, although rarely among adults, to engage in swimming behavior.

Overall, our data suggest that shifts in microclimate selection and swimming effect an animal’s body temperature patterns, and the animal’s ability to buffer itself from heat even when they have access to drinking and swimming water. Such behavioral adaptations would undoubtedly become increasingly important in the absence of available drinking water (i.e., drought), a frequent occurrence for vervet populations in South Africa (Pasternak et al., 2013; Hoffman, Carrick, Gillson & West, 2009; Young et al. in revision). Climate change will not only expose animals to progressively warmer climates, but there will also be an increase in the frequency of periods of drought (Engelbrecht et al., 2015). With limited water resources, and an increased demand on evaporative cooling to keep cool, mammals will become increasingly dependent on the use of behavioral adjustments – i.e., the selection of microclimates where air temperature is lower than body temperature – to help alleviate the autonomic costs of maintaining homeostasis. This could be especially true for mammals of relatively small body mass, such as the primates, as their smaller surface area to volume ratio and lower thermal inertia makes them gain environmental heat at a faster rate than do larger mammals (Fuller et al., 2016).

Knowing how primates respond to changes in the thermal environment will help us understand how climate change is likely to affect species survival in an order already facing substantial pressure (Estrada et al., 2017). The evidence suggests that primates are able to balance the competing demands of their environment, and are able to adjust flexibly the amount of time that they devote to different activities, including foraging, resting, social and thermoregulatory behaviors (Dunbar, Korstjens & Lehmann, 2009; Korstjens et al., 2010, Lehmann et al., 2010; McFarland & Majolo, 2013; McFarland et al., 2014, Hetem et al., 2014; Fuller et al. 2016; McFarland et al., 2017; Ostner & Schulke, 2018). Nevertheless, climate change constrains species' biogeographic distributions, not only through its direct effect on a species' behavior and physiology (Korstjens et al., 2010, Lehmann, Korstjens & Dunbar, 2010; Hetem et al. 2014; Fuller et al., 2016), but also via a negative impact on plant productivity and subsequent habitat loss (Campos et al., 2017; Hill & Winder., 2019). Even for those species considered to be the most ecologically flexible (e.g., baboons), habitat loss as a result of climate change will threaten their distribution and survival (Campos et al., 2017; Estrada et al., 2017; Fuchs, Gilbert & Kamilar, 2017; Hill & Winder, 2019).

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Conflicts of interest

The authors declare no conflicts of interest.

Data sharing

The data and analysis code that support the findings of this study are openly available on figshare at https://doi.org/10.6084/m9.figshare.8089220 [to be published at time of manuscript publication].

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Figure legends

Figure 1. The mean daily body temperature (T_b: °C) pattern of all of the vervet monkeys (N = 21) that were equipped with temperature-sensitive data loggers and the corresponding mean black globe temperature (°C) over (a) the one-year study period, and (b) January only.

Figure 2. The difference between before- and after-drinking vervet monkey body temperatures (°C) over an immediate, 30-minute and 60-minute post-drinking time frames. Each dot denotes a single drinking event.

Figure 3. The 24 h body temperature (°C) profile of a one of our data-logged vervet monkeys that swam (blue line), and one that did not swim (black line) in relation to the time of day and the black globe temperature (°C) (dotted line). The black arrow denotes the start of a 45 s swimming event. Both the swimmer (3.2 kg) and the non-swimmer (3.8 kg) were adult females living in the same group.