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ORIGINAL ARTICLE

Differential responses of non-human primates to seasonal temperature fluctuations

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Abstract

Non-human primates (NHPs) can adapt to conditions outside of their natural habitat and climatic ranges but this can be influenced by inherent evolutionary traits or plasticity of species that evolved in diverse environmental conditions. In this study, we investigated how five species of NHPs that have natural distributions across a range of climatic conditions responded to seasonal temperature changes in a captive environment. The activity levels of NHPs were affected by temperature changes over the season, where activity levels were generally reduced at the lower and higher temperature ranges. Species that are naturally found within narrower and warmer climatic ranges, compared to those found in colder environments with wider fluctuations in temperature, showed more marked changes in activity levels in response to temperature changes. In lower temperature conditions, three out of five species showed significantly lower activity levels; whereas in higher temperature conditions, the activity levels of all species did not significantly decrease. The frequency of thermoregulation behaviours was higher, and use of artificial thermoregulatory sources lower, for species that did not substantially adjust their activity levels in different temperature conditions. Our results suggest that NHPs largely retained the evolutionary traits related to thermoregulation, according to the different ambient conditions they evolved in and may have low behavioural plasticity in adapting to conditions outside of their natural ranges. These results provide insights for improving conservation and captive management and may have implications for understanding NHP resilience to the increasing impact of global climate change.

Keywords Activity · Adaptation · Behavioural plasticity · Captive primates · Thermoregulation

Introduction

The maintenance of core body temperature is an important aspect for mammalian survival (Randall et al. 1997; Terrien et al. 2011). Non-human primates (hereinafter referred to as primates) are thought to have relatively lower tolerance for colder climates compared to many other mammals (Fleagle and Gilbert 2006). Changes in ambient temperature can be important physiological stressors for primates, which influences their metabolic strategies in response to thermoregulatory pressures. These can be expressed through seasonal hormonal changes in cortisol and thyroid hormones which affect activity, ranging and foraging patterns, as well as social interactions (e.g. Weingrill et al. 2004; McFarland and Majolo 2013; McFarland et al. 2015; Cristobal-Azkarate et al. 2016; Thompson et al. 2017).

Primate species have evolved specific adaptations to climate and seasonality (Reed and Fleagle 1995; Ganzhorn et al. 2003), such as hibernation in the fat-tailed dwarf lemur (*Cheirogaleus medius*) (Fietz and Dausmann 2006), torpor and other physiological adaptations in grey mouse lemurs (*Microcebus murinus*) (Schmid and Speakman 2000) and reddish-grey mouse lemur (*Microcebus griseorufus*) (Kobbe et al. 2014). Other physiological mechanisms can include sweating, panting and shivering (reviewed in Campos and Fedigan 2009), and behavioural thermoregulation through adjustments to activity and posture (ruffed lemur *Varecia variegata*, Morland 1993; black-and-gold howler monkey *Alouatta caraya*, Bicca-Marques and Calegaro-Marques 1998; baboon *Papio* spp., Hill 2006; Van Doorne et al. 2010; collared lemur *Eulemur collaris*, Donati et al. 2011; Yunnan

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snub-nosed monkey *Rhinopithecus bieti*, Grueter et al. 2013; vervet monkey *Chlorocebus pygerythrus*, McFarland et al. 2014), social thermoregulation (red-fronted lemur *Eulemer fulvus fulvus*, Ostner 2004; Japanese macaque *Macaca fuscata*, Hanya et al. 2007, 2018; *R. bieti*, Li et al. 2010 black-fronted titi monkey *Callicebus nigrifrons*, Gestich et al. 2014), and microhabitat selection (*A. caraya*, Bicca-Marques and Calegaro-Marques 1998; *Papio* spp., Pochon 2000; Hill 2004, 2006; *M. fuscata*, Hanya et al. 2007; black howler monkey *Alouatta pigra*, Aristizabal et al. 2018). These adaptations have been mainly shown within the natural climatic ranges of primate species, where the importance of adaptations like behavioural thermoregulation generally increases in harsher climatic conditions.

For wild primate species, food resource fluctuation is an important interacting factor for seasonal variations in activity and cost of thermoregulation. Studies have shown that food quality and availability in different seasons influenced activity budget and these are related to thermoregulatory costs (e.g. *M. fuscata*, Agetsuma 1995, Hanya 2004, Tsuji 2010; Arunachal macaque *Macaca munzala*, Mendiratta et al. 2009; *E. collaris*, Donati et al. 2011; Barbary macaque *Macaca sylvanus*, Majolo et al. 2013). A comparative study on multiple species of primates by Korstjens et al. (2010) showed that resting time was determined by diet and annual temperature as well as by temperature variation. These effects had particular constraints on folivorous primates because of the demands of digesting high-fibre foods. This is because the process of digestion confers an energetic cost according to diet, food quality and specific gastrointestinal adaptations of different primate species (Lambert 1998; Milton 1998).

Primates in captivity are not constrained by seasonal fluctuations in food resources. However, like their conspecifics in the wild, temporal environmental variations in ambient temperature and photoperiod can exert effects on activity rhythms, energetics and thermoregulatory processes (Heldmaier et al. 1989; Morland 1993; Erkert and Kappeler 2004). For optimal survival and reproduction in captivity, primates have to adapt to environmental conditions that could be very different from the conditions that they evolved in. For example, for species that reproduce seasonally, specific environmental cues are needed for successful reproduction (Di Bitetti and Janson 2000; Jansen and Verdolin 2005; Van Schaik and Brockman 2005). Exposure to extreme temperature differences not found in their natural distribution ranges had also been suggested as one of the reasons some primate species like the douc langur (*Pygathrix nemaeus*) and proboscis monkey (*Nasalis larvatus*) could not be successfully maintained in Europe and North America (Lippord 1989; Lhota et al. 2019). Thermal stress on primates housed in conditions outside of their thermoneutral zones also has profound effects on their welfare (Litchfield et al. 2011). It is expected that interspecific differences in resilience to temperature exist between primate clades/species. Sensitivity to changes in environmental conditions could stem from phylogenic differences, according to inherent evolutionary traits (Troisi and Schino 1986), as well as how well species can adjust their behaviours in order to adapt to local conditions (Van Schaik 2013).

Although direct empirical evidence for the impact of climate change on primates is scant, numerous primates are expected to experience changing climatic conditions, increasing their vulnerability under the impact of other anthropogenic changes (Graham et al. 2016; Estrada et al. 2017; Carvalho et al. 2019). Studies on the indirect effects of ambient temperature, for example, how it affects forest productivity, have shown a general decrease in quality and distribution of food resources (Del Grosso et al. 2008). A decline in colobine abundance may also be explained by the decrease in protein-to-fibre ratio of food plants, induced by environmental changes over the past 30 years (Rothman et al. 2015; Rothman and Bryer 2019). Studies on the effects of changing climates on temperate forest species have also suggested historical range contraction and fragmentation due to changes in temperature and precipitation (Nüchel et al. 2018; Zhao et al. 2019). It is difficult to investigate the direct effect of climate changes on wild primates, as significant detectable changes can occur over extended periods for long-lived mammals. However, primate species that are brought into captivity, into conditions that differ from their natural habitat ranges, can offer some insights into the behavioural and physiological responses of primates to temperature changes.

In this study, we examined five species of primates from varying climate conditions in their natural distribution ranges but housed in the same environment in captivity. We hypothesized that primate species would show differential flexibility in adapting to fluctuating temperatures, according to the range of temperatures within their natural distribution ranges. Accordingly, we predict that species found in colder climates with wider temperature ranges would be able to better adjust to temperature changes without significant changes in activity. These species would use more behavioural thermoregulation strategies i.e. higher frequency and repertoire of thermoregulation behaviours. This would suggest that primates largely retain the evolutionary traits associated with thermoregulation, according to the climatic conditions they are naturally found in. Conversely, species found in warmer climates with narrower temperature ranges would be less able to adjust to temperature changes without significant changes in activity. These species would rely more on artificial thermoregulation sources if they do not employ more behavioural thermoregulation strategies.

This would indicate low plasticity in coping with different climatic conditions.

Methods

Study subjects

Five species of primates at Guangzhou Zoo, China were included in this study (Table 1). The study species represented primates found on different continents, at different latitudinal and climatic ranges and with different body sizes. The pig-tailed macaque (*Macaca nemestrina*) and white-headed capuchin (*Cebus albifrons*) are found in relatively warmer climates where, within their distribution ranges, mean minimum temperatures are close to 20 °C and mean maximum temperatures slightly above 30 °C. The lion-tailed macaque (*Macaca silenus*) and De Brazza's monkey (*Cercopithecus neglectus*) are found in climates that have lower mean minimum temperatures of below 20 °C and mean maximum temperatures of close to 30 °C. Both species have also been recorded in lower temperature conditions, *M. silenus* (12 °C) (Kurup and Kumar 1993) and *C. neglectus* (11 °C) (Walker and Sajita 2011). The ring-tailed lemur (*Lemur catta*) has a distribution range with wide variation in temperatures, from close to 10 °C to well above 30 °C. The species has also been recorded at temperatures ranging from 3 °C to above 40 °C (Sussman 1991; Kamilar and Muldoon 2010; Kelley et al. 2016).

Study site

This study was conducted in Guangzhou city, Guangdong province located in southeastern China. The climate is humid subtropical with historical monthly averages ranging from 13.9 °C in January to 28.9 °C in July (China Meteorological Administration, www.cma.gov.cn). The typical minimum and maximum temperatures in the past decade were 5 °C and 34 °C (Yang et al. 2013), but extreme temperatures of 0 °C to 39.1 °C have been recorded (Extreme World Temperatures, https://www.mherrera.org/temp.htm). During our study in 2018, the lowest mean temperature was 9.9 °C in January and highest mean temperature was 33.5 °C in July (Fig. 1).

At the study site at Guangzhou Zoo, all study animals were housed in semi-open enclosures of similar sizes in a building block with six adjacent animal enclosures. The outdoor enclosures are glass-fronted with open tops and

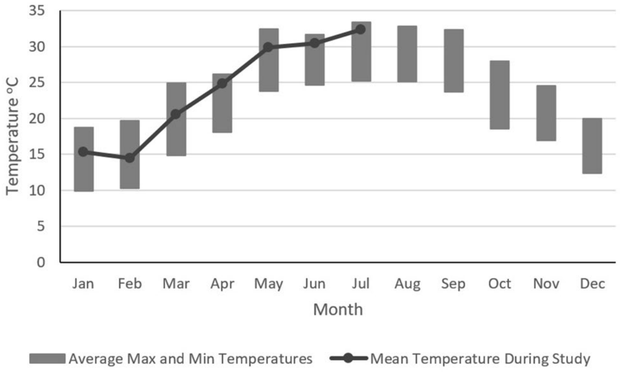

Fig. 1 Maximum and minimum average temperatures and mean temperature sampled during this study

Table 1 Age–sex class, average body mass, region, latitudinal range and temperature range of species in this study

Species	No. of individuals and age class	Average body mass (kg)	Region/latitudinal range	Temperature range (mean min and max)
Pig-tailed macaque (*Macaca nemestrina*)	1 adult male, 1 adult female	8.89	South East Asia 5.9° S to 10.9° N	20.7–31.2 °C
White-headed capuchin (*Cebus albifrons*)	1 adult male, 2 adult females	2.74	South America 14.6° S to 11.7° N	19.9–31.0 °C
Lion-tailed macaque (*Macaca silenus*)	1 adult male, 1 adult female	7.50	India 8.3° N to 14.4° N	17.6–28.9 °C
De Brazza's monkey (*Cercopithecus neglectus*)	1 adult male, 1 adult female, 2 juveniles	5.74	Central Africa 8.9° S to 9.7° N	18.1–30 °C
Ring-tailed lemur (*Lemur catta*)	1 adult male, 2 adult female, 3 juveniles	2.21	Madagascar 25.6° S to 20.8° S	12.4–34.2 °C

Latitudinal range limits were estimated from IUCN Red List distribution maps https://www.iucnredlist.org/. Temperature ranges were estimated from overlays of distribution maps over climate data from https://worldclim.org, accounting for elevational differences using Digital Elevation Models from https://databasin.org. Elevation ranges: *M. nemestrina* (0–1900 m) (Yanuar et al. 2009); *C. albifrons* (0–2000 m) (Defler 1979); *M. silenus* (100–1800 m) (Kumar et al. 2008); *C. neglectus* (0–2200 m) (Struhsaker et al. 2008); *L. cattta* (0–2600 m) (Goodman and Langrand 1996). Data on body mass from Galán-Acedo et al. (2019)

the enclosures for each species separated by wire fencing. The dimensions of the outdoor enclosures range from 6.2 m length × 3.9–4.8 m wide × 3.6 m height. These enclosures have grass-tufted substrates, some tree vegetation (for most enclosures, a single tall tree) and a raised platform that is sheltered by a roof structure. An indoor enclosure is connected to each outdoor enclosure and accessible through a door. The dimensions of the indoor enclosures range from 3.6–4.2 m length × 2.8 m wide × 2.6 m height. The indoor enclosures are freely accessible to the animals. During colder months, heaters are provided in the indoor enclosures and during the hotter months, mist sprays are activated at regular intervals in the outdoor enclosures.

Behaviour observation and climatic variables

We collected behavioural data using video cameras (Sony™ HDR-CX900). Observations were conducted over seven months from 2 January to 30 July 2018. We observed the behaviours of all available subjects of each species and collected 36 h of data for each species, totalling 180 observation hours. Observations were conducted during the hours of 9 am to 12 noon and from 1 to 4 pm. However, observation times were not entirely balanced across temperature ranges, owing to unforeseen situations where observations were stopped because of inclement weather. To control for additional confounding variables, we discarded data sets where there was rain. We conducted additional observations to make up for lost hours of observation, so as to balance the data set as much as possible.

We analysed the video recordings using Noldus Observer XT 13.0 and according to the ethogram in Table 2. Scan sampling (Altmann 1974) at 1-min intervals was used to analyse data in the ethogram categories “general behaviours” and “enclosure use”. Behaviours were only observed in the outdoor enclosure as the subjects were not visible once they entered the indoor enclosure. We calculated the total percentage of time spent by each species on active behaviours and in the outdoor enclosure versus the indoor enclosure. These were divided into hourly data sets, where all behaviours were considered active with the exception of the category “rest”. All-occurrence sampling was used for behaviours under the category “thermoregulation behaviours” and expressed as frequency per hour. Climatic variables were collected using a temperature/humidity logger (AZ® 88163), which recorded data at 5-min intervals. This logger was placed at a fixed location near the subjects’ enclosures. Temperature data was similarly split into hourly data sets which corresponded to the behavioural data sets.

Statistical analysis

We used mixed-effects polynomial regression to test the effect of ambient temperature on time spent active. A polynomial function was used as activity and temperature fluctuations followed a circadian pattern. For each species, we constructed polynomial models up to a degree of three and used sequential analysis of variance to determine the polynomial order that provided the best fit model. Behavioural data were split into hourly time intervals for analysis. As time of day could follow a circadian rhythm exerting an effect on activity that is independent of temperature effects, we tested for the random effect of time of day using a likelihood ratio test. This was also used to

Table 2 Ethogram of general activity, thermoregulation behaviours and exhibit use used for analysis in this study

Behaviour/exhibit use	Description
General behaviours	
Rest	Any inactivity in a stationary and relaxed posture including sleep with eyes closed
Locomotion	Any movement (walk, run, climb, jump, etc.)
Feed/forage	Any activity associated with acquisition and ingestion of food, including manipulation, manual and oral food processing
Groom	Autogroom and allogroom (as actor) by licking, nibbling or picking the surface of the body with fingers
Others	Other behaviours like swing, hang, copulation, play, drink, urination and defecation
Thermoregulation behaviours	
Postural	Hunched sitting position, may include variations like curling into a ball with the tail wrapped around or with upper limbs crossed or tucked under lower limbs; sun basking with upper limbs outstretched (unique to ring-tailed lemurs)
Social	Huddling (defined as trunk–trunk contact with other individuals) and in a stationary position with no limb movements
Enclosure use	
Outdoor	Where the subject could be observed in the outdoor exhibit
Indoor	Where the subject could not be observed in the outdoor exhibit

Thermoregulation behaviours adapted from Paterson (1981), Morland (1993), Hanya et al. (2007), Donati et al. (2011) and Gestich et al. (2014)

control for pseudo-replication for data sets that were split by time of day. We used linear regression to test the effect of ambient temperature on time spent active, above and below temperatures of peak activity levels. We tested for differences in frequency of behavioural thermoregulation between species, using one-way analysis of variance (ANOVA) with post hoc Tukey-HSD (honestly significant difference) tests. We used two-way ANOVA to test for the effect of temperature on enclosure use and for any significant interacting effects between temperature and species; and temperature and enclosure use. For this analysis, we transformed the activity data into categories of different temperature ranges: < 10 °C, > 10 to 20 °C, > 20 to 30 °C and > 30 °C. We tested the relationship between frequency of behavioural thermoregulation and enclosure use; as well as temperature, using Pearson's correlation. All data were checked for normality using Kolmogorov–Smirnov tests. We tested for homogeneity of variance using Bartlett's test for groups of data used in the ANOVA procedures. Analyses were performed with the R statistical package, version 3.1.2 (R Development Core Team, R Foundation for Statistical Computing, Vienna; https://www.rproject.org/). Statistical significance was set at $p < 0.05$.

Results

Effect of temperature on activity

There was a significant effect of ambient temperature on the activity of pig-tailed macaques using a best fit quadratic model ($F_{(2,33)} = 10.55$, $p < 0.001$) with time of day accounting for a variance of 6.1% which was significant ($\chi^2 = 7.704$, $p = 0.021$). There was a significant effect of ambient temperature on activity of capuchins using a best fit quadratic model ($F_{(2,33)} = 19.501$, $p < 0.001$) with time of day accounting for a variance of 11.5% which was significant ($\chi^2 = 27.593$, $p < 0.001$). There was a close to significant effect of ambient temperature on the activity of lion-tailed macaques using a best fit quadratic model ($F_{(2,33)} = 2.934$, $p = 0.067$) with time of day accounting for a variance of 4.2% which was significant ($\chi^2 = 7.805$, $p = 0.020$). There was no significant effect of ambient temperature on the activity of De Brazza's monkeys using a best fit cubic model ($F_{(2,33)} = 2.173$, $p = 0.110$) with time of day accounting for a variance of 4.8% which was significant ($\chi^2 = 6.281$, $p = 0.043$). There was no significant effect of ambient temperature on the activity of ring-tailed lemurs using a best fit cubic model ($F_{(2,33)} = 0.364$, $p = 0.779$) with time of day accounting for a variance of 1.42% which was not significant ($\chi^2 = 0.978$, $p = 0.613$). Graphs depicting the relationships between percentage of active time and temperature are shown in Fig. 2a–e.

Below temperatures of peak activity, there was a significant effect of temperature on the activity of pig-tailed macaques ($F_{(1,26)} = 20.25$, $p < 0.001$, $R^2 = 0.420$), capuchin monkeys ($F_{(1,26)} = 16.34$, $p < 0.001$, $R^2 = 0.346$) and lion-tailed macaques ($F_{(1,27)} = 4.31$, $p = 0.047$, $R^2 = 0.127$), but no significant effect of temperature on the activity of De Brazza's monkeys ($F_{(1,14)} = 1.129$, $p = 0.306$, $R^2 = 0.075$) and ring-tailed lemurs ($F_{(1,12)} = 0.688$, $p = 0.428$, $R^2 = 0.071$).

Above temperatures of peak activity, there were no significant effects of temperature on the activity of all species: pig-tailed macaques ($F_{(1,6)} = 0.735$, $p = 0.416$, $R^2 = -0.030$), capuchin monkeys ($F_{(1,6)} = 3.714$, $p = 0.102$, $R^2 = -0.255$), lion-tailed macaques ($F_{(1,5)} = 0.347$, $p = 0.582$, $R^2 = -0.122$), De Brazza's monkeys ($F_{(1,18)} = 0.133$, $p = 0.719$, $R^2 = -0.045$) and ring-tailed lemurs ($F_{(1,20)} = 1.186$, $p = 0.289$, $R^2 = -0.144$).

Behavioural thermoregulation

The frequency of thermoregulation behaviour was significantly different between species ($F_{(4,175)} = 9.526$, $p < 0.001$) (Fig. 3). Post-hoc tests showed that ring-tailed lemurs spent significantly more time on thermoregulation behaviours compared to pig-tailed macaques ($p < 0.001$), capuchin monkeys ($p < 0.001$) and lion-tailed macaques ($p < 0.001$). De Brazza's monkeys spent significantly more time in behavioural thermoregulation compared to pig-tailed macaques ($p < 0.01$) and lion-tailed macaques ($p = 0.043$). The frequency of thermoregulation increased with decreasing temperature (Pearson Correlation: $r = -0.442$, $n = 178$, $p < 0.01$).

Effect of temperature on enclosure use

Enclosure use was significantly different between species ($F_{(4,170)} = 14.524$, $p < 0.001$) (Fig. 4). The relationship between enclosure use and species was independent of temperature differences with a non-significant interaction effect between species and temperature ($F_{(4,170)} = 2.178$, $p = 0.059$). Post hoc Tukey-HSD tests showed that pig-tailed macaques used the indoor enclosure significantly more than ring-tailed lemurs ($p < 0.001$), lion-tailed macaques ($p < 0.001$) and De Brazza's monkey ($p = 0.02$); Capuchins used the indoor enclosure significantly more than ring-tailed lemurs ($p < 0.001$) and lion-tailed macaques ($p < 0.01$); and lion-tailed macaques used the indoor enclosure significantly less than De Brazza's monkey ($p < 0.01$).

Enclosure use was significantly different over temperature ranges ($F_{(4,170)} = 5.116$, $p = 0.025$). The relationship between enclosure use and temperature is dependent on species differences with a significant interaction effect between temperature and species ($F_{(4,170)} = 11.890$, $p < 0.001$). Use of indoor enclosure was

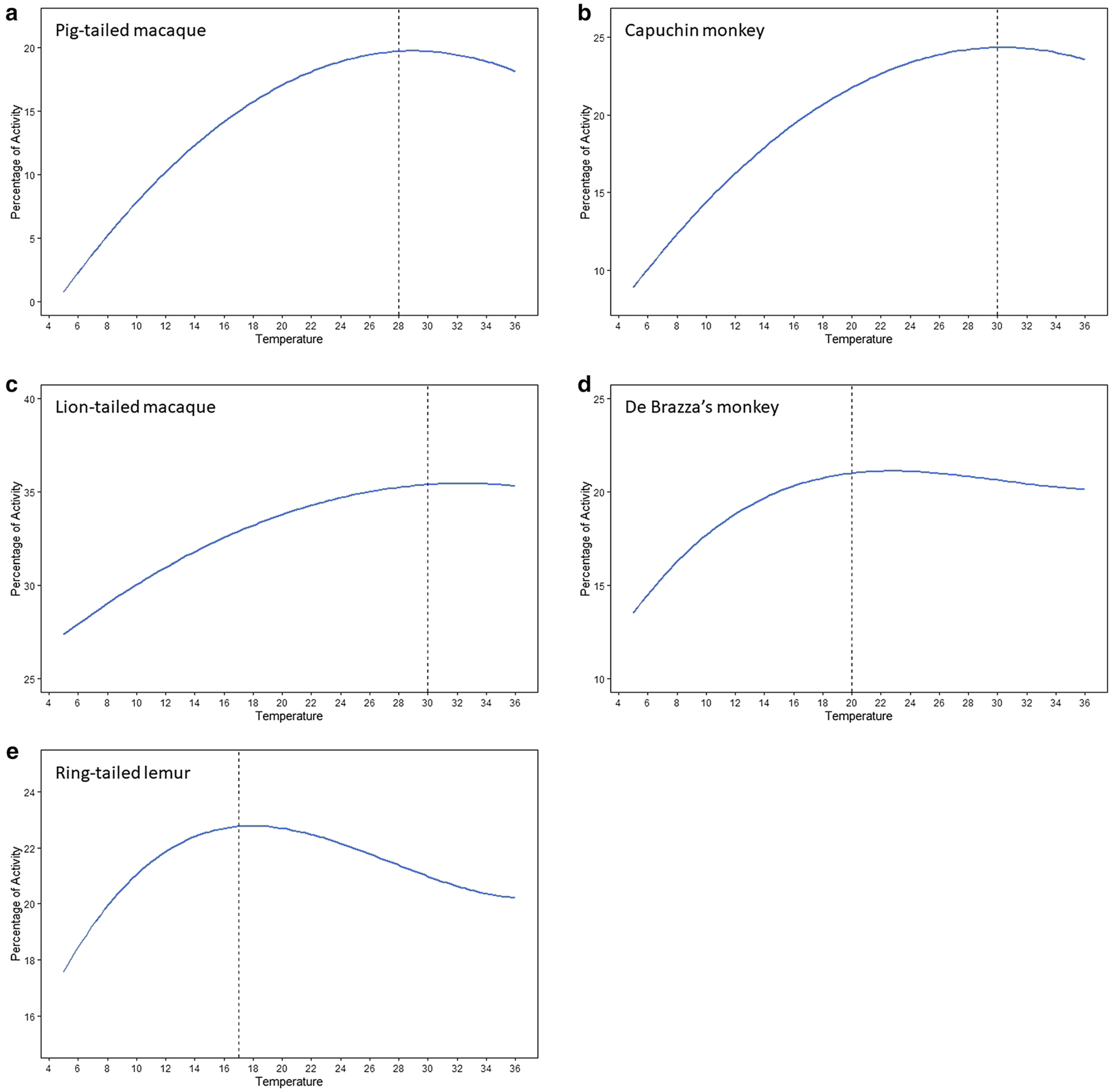

Fig. 2 Graphical models of mixed-effects polynomial regression for the effect of temperature on percentage of activity. Peak in activity levels indicated by vertical dotted lines

significantly higher at temperatures below 10 °C compared to 20–30 °C ($p = 0.024$), and significantly higher at temperatures over 30 °C compared to 10–20 °C ($p < 0.01$) and 20–30 °C ($p < 0.001$). There was a negative correlation between enclosure use and frequency of behavioural thermoregulation (Pearson correlation $r = -0.198$, $n = 178$, $p < 0.01$).

Discussion

The activity levels of primate species in this study were affected by temperature changes over the season, where activity levels were generally reduced at the lower and higher temperature ranges. At the lower end of the

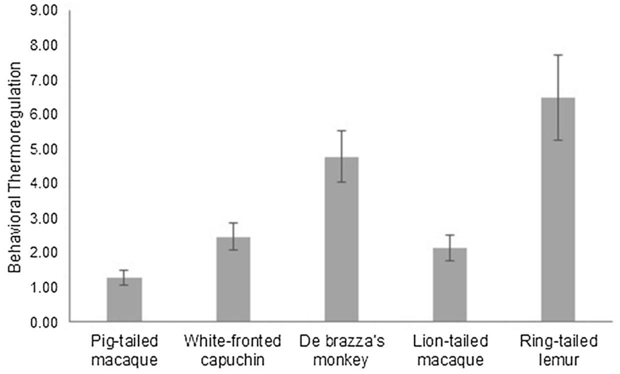

Fig. 3 Frequency (per hour) of thermoregulation behaviours

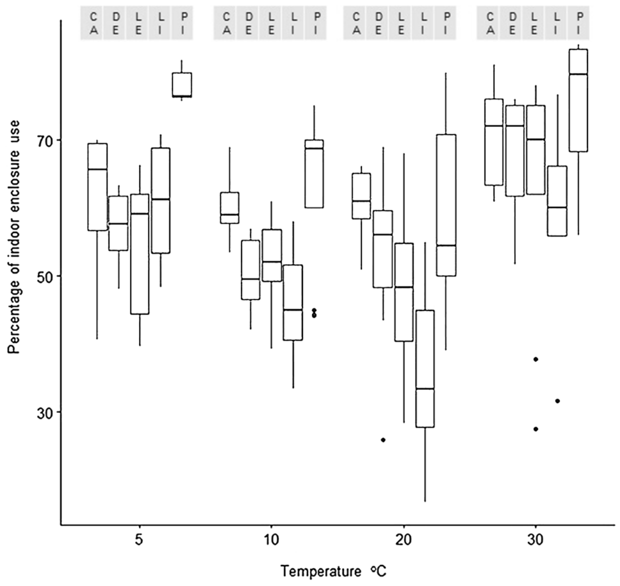

Fig. 4 Percentage of indoor enclosure use at different temperature ranges. CA white-headed capuchin, DE De Brazza's monkey, LE ring-tailed lemur, LI lion-tailed macaque, PI pig-tailed macaque

temperature gradient, pig-tailed macaques, white-fronted capuchins and lion-tailed macaques showed significant decreases in activity levels when temperatures decreased. At the higher end of the temperature gradient, all species did not show significant decreases in activity levels when temperatures increased. Significant effects of temperature on the activities of pig-tailed macaques and white-fronted capuchins supported our hypothesis that species from warmer and narrower climatic distribution ranges responded more to temperature changes by adjusting their activity levels. This hypothesis was further supported by findings that their frequency of thermoregulation behaviour was low and they significantly used more artificial thermoregulatory sources and the indoor enclosure to mitigate the effects of low ambient temperature. Although it could also be argued that higher utilization of the indoor enclosure indicated a positive adaptation, it would seem counterintuitive to suggest that this behaviour represented natural resilience when compared to other typical thermoregulatory behaviours and homeostatic regulation of body temperature. In contrast, the activities of De Brazza's monkeys and ring-tailed lemurs were not significantly influenced by temperature changes. This was again related to the fact that they showed higher frequencies of behavioural thermoregulation and less use of artificial thermoregulatory sources. The lion-tailed macaques showed a close to positive effect of temperature on their activity, although they are found within similar climatic ranges as the De Brazza's monkey. This effect was mainly contributed by significantly lower activity levels at lower temperatures. Consequently, this species showed low frequency of thermoregulation behaviours and higher use of the indoor enclosure. The peak in activity for all species was from approximately 17 °C to 30 °C, which could suggest an optimal temperature range for primate species to be suitably maintained outside their natural distribution ranges. Overall, our results supported that seasonal activity patterns of the primates in this study are likely related to inherent adaptations to temperatures found in their native climatic conditions.

There are several confounding factors that should be considered in the interpretation of our results. One factor is the variable group sizes of our study species, which could facilitate social thermoregulation in groups with more individuals and limit it in groups with fewer individuals. Most notably, the lion-tailed and pig-tailed macaque groups only consisted of two individuals which limited their use of huddling as a social thermoregulation strategy, often documented for other wild macaque species that experience temperature climates (e.g. *M. fuscata*, Hanya et al. 2007; *M. sylvanus*, Campbell et al. 2018). Although huddling had also been documented for subtropical/tropical species (e.g. Bonnet macaque *Macaca radiata*, Silk 1994; Sulawesi crested macaque *Macaca nigra*, Thierry et al. 2000), these were mostly in the context of social interactions. Hence, it could also be the case that our two species of study macaques did not extensively adopt huddling as a thermoregulation strategy, even in natural conditions. In contrast, lemur species can exhibit a wide range of thermoregulation behaviours like huddling (*V. variegata*, Morland 1993; *Hapalemur griseus alaotrensis*, Mutschler 2002; *E. fulvus fulvus*, Ostner 2004; Southern bamboo lemurs *Hapalemur meridionalis*, Eppley et al. 2017), with sun basking shown to be of particular importance for *L. catta* under cold weather conditions (Kelley et al. 2016). Indeed, ring-tailed lemurs in our study were found to extensively use strategies such as sun basking when their enclosures were exposed to direct sunlight. This suggests that behavioural thermoregulatory traits of wild conspecifics in their natural habitats are retained in captivity. To improve our understanding of behavioural thermoregulation strategies, another factor that can be examined in greater depth is how changes in body posture can aid or inhibit heat loss to improve thermoregulation efficiency (e.g. Paterson 1981; Dasilva 1993). Measurements of the effects of ambient temperature on surface temperature can be aided by thermal imaging technology, as increasingly used in recent studies (e.g. Tattersall and Cadena 2010; Ioannou et al. 2015; Guo et al. 2018), with comparisons to body temperature using implanted temperature loggers (e.g. Lubbe et al. 2014; Bethge et al. 2017; Thompson et al. 2017).

In this study, we also did not consider the possible effects of body mass differences between the study species that may affect energy expenditure and thermoregulation efficiency in different temperature conditions. Basal metabolic rate is expected to increase with larger body mass (Pontzer et al. 2014) and smaller body mass is beneficial for thermoregulation in warmer climates (Bergmann 1847; Gardner et al. 2011). The De Brazza's monkey, lion-tailed and pig-tailed macaques used in this study were much larger than the white-fronted capuchin and ring-tailed lemur. However, activity levels in relation to temperature changes did not suggest a body mass effect. The activity levels of capuchins, pig-tailed macaques and lion-tailed macaques showed significant relationships to temperature while the De Brazza's monkeys and ring-tailed lemurs did not. At higher temperatures, all species also did not show significant activity responses to increasing temperature despite differences in body mass.

Food resource fluctuation is an important factor for seasonal variations in activity and cost of thermoregulation in wild primates. In the absence of significant food resource fluctuation in captivity, we could better examine the independent effect of temperature on seasonal variation of activity. However, another factor that could be better examined is the autonomic thermoregulatory mechanisms related to digestive physiology, which could confer differential energetic costs independent of the effect of temperature. Although lower ambient temperatures generally confer additional energetic costs (Satinoff 2011; McFarland et al. 2014; Sha et al. 2018), different gastrointestinal adaptations of primate species (Lambert 1998; Milton 1998) meant that the interaction between temperature and the energetic cost of digestion could differ. Further investigations into this aspect, for example, by comparing the autonomic energy expenditure of foregut- and hindgut-fermenting primates in different temperature conditions, is needed to better explain our current findings. In addition, some primate species have wide distribution in different habitats at different elevation zones (and thus climatic conditions); intraspecific variations should also be further investigated in both wild and captive primate species. The time spent in captivity can also influence the acclimatization of primates to seasonal temperatures outside of their native temperature ranges and should be considered in future studies.

In summary, our study provided preliminary insights into how several primate species could differentially respond to climatic conditions outside of their natural distribution ranges. Our results seemed to suggest a retention of evolutionary traits from their natural climatic distribution ranges and generally low behavioural plasticity in response to fluctuations in climatic conditions. These results provide a basis for further investigations into the physiological mechanisms that influence temperature adaptability, where primates can be used as a model for long-lived mammals.

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Compliance with ethical standards

Ethical approval All research conducted in this study adhered to international guidelines for the ethical treatment of animals. No invasive experiments were conducted. The authors declare that there are no financial, professional or personal conflicts of interest related to this study.

References

Agetsuma N (1995) Dietary selection by Yakushima macaques (*Macaca fuscata yakui*): the influence of food availability and temperature. Int J Primatol 16:611–627

Altmann J (1974) Observational study of behavior: sampling methods. Behaviour 49:227–266

Aristizabal JF, Lévêque L, Chapman CA, Serio-Silva JC (2018) Impacts of temperature on behaviour of the Mexican endangered black howler monkey *Alouatta pigra* Lawrence, 1933 (Primates: Atelidae) in a fragmented landscape. Acta Zool Bugarica 70:377–382

Bergmann C (1847) Uber die Verhältnisse der warmeokonomiedie Thiere zu ihrer grösse. Göttinger Studien 3:595–708.

Bethge J, Wist B, Stalenberg E, Dausmann K (2017) Seasonal adaptations in energy budgeting in the primate *Lepilemur leucopus*. J Comp Physiol B 187:827–834

Bicca-Marques JC, Calegaro-Marques C (1998) Behavioral thermoregulation in a sexually and developmentally dichromatic neotropical primate, the black-and-gold howling monkey (*Alouatta caraya*). Am J Phys Anthropol 106:533–546

Campbell LA, Tkaczynski PJ, Lehmann J, Mouna M, Majolo B (2018) Social thermoregulation as a potential mechanism linking sociality and fitness: Barbary macaques with more social partners form larger huddles. Sci Rep 8:6074

Campos FA, Fedigan LM (2009) Behavioral adaptations to heat stress and water scarcity in white-faced capuchins (*Cebus *capucinus*) in Santa Rosa National Park, Costa Rica. Am J Phys Anthropol 138:101–111

Carvalho JS, Graham B, Rebelo H, Bocksberger G, Meyer CFJ, Wich S, Kühl HS (2019) A global risk assessment of primates under climate and land use/cover scenarios. Glob Change Biol 25:3163–3179

Cristóbal-Azkarate J, Maréchal L, Semple S, Majolo B, MacLarnon A (2016) Metabolic strategies in wild male Barbary macaques: evidence from faecal measurement of thyroid hormone. Biol Lett 12:20160168

DaSilva GL (1993) Postural changes and behavioural thermoregulation in *Colobus polykomos*: the effect of climate and diet. Afr J Ecol 31:226–241

Defler TR (1979) On the ecology and behavior of *Cebus albifrons* in eastern Colombia: I. Ecol Primates 20:475–490

Del Grosso S, Parton W, Stohlgren T, Zheng D, Bachelet D, Prince S, Hibbard K, Olso R (2008) Global potential net primary production predicted from vegetation class, precipitation, and temperature. Ecology 89:2117–2126

Di Bitetti MS, Janson CH (2000) When will the stork arrive? Patterns of birth seasonality in neotropical primates. Am J Primatol 50:109–130

Donati G, Ricci E, Baldi N, Morelli V, Borgognini-Tarli SM (2011) Behavioral thermoregulation in a gregarious lemur, *Eulemur collaris*: effects of climatic and dietary-related factors. Am J Phys Anthropol 144:355–364

Eppley TM, Watzek J, Dausmann KH, Ganzhorn JU, Donati G (2017) Huddling is more important than rest site selection for thermoregulation in southern bamboo lemurs. Anim Behav 127:153–161

Erkert HG, Kappeler PM (2004) Arrived in the light: diel and seasonal activity patterns in wild Verreaux's sifakas (*Propithecus v. verreauxi*; Primates: Indriidae). Behav Ecol Sociobiol 57:174–186

Estrada A, Garber PA, Rylands AB, Roos C, Fernandez-Duque E, Di Fiore A, Nekaris KA, Nijman V, Heymann EW, Lambert JE, Rovero F (2017) Impending extinction crisis of the world's primates: why primates matter. Sci Adv 3:e1600946

Fietz J, Dausmann KH (2006) Big is beautiful: fat storage and hibernation as a strategy to cope with marked seasonality in the fat-tailed dwarf lemur (*Cheirogaleus medius*). In: Gould L, Sauther ML (eds) Lemurs: ecology and adaptation. Springer, New York, pp 97–110

Fleagle JG, Gilbert CC (2006) The biogeography of primate evolution: the role of plate tectonics, climate and chance. In: Fleagle JG, Lehman SM (eds) Primate biogeography. Springer, Boston, pp 375–418

Galán-Acedo C, Arroyo-Rodríguez V, Andresen E, Arasa-Gisbert R (2019) Ecological traits of the world's primates database (Version 3). Zenodo. https://doi.org/10.5281/zenodo.2600338

Ganzhorn JU, Klaus S, Ortmann S, Schmid J (2003) Adaptations to seasonality: some primate and non-primate examples. In: Pereira ME, Kappeler PM (eds) Primate life histories and socioecology. University of Chicago Press, Chicago, pp 132–148

Gardner JL, Peters A, Kearney MR, Joseph L, Heinsohn R (2011) Declining body size: a third universal response to warming? Trends Ecol Evol 26:285–291

Gestich CC, Caselli CB, Setz EZ (2014) Behavioural thermoregulation in a small Neotropical primate. Ethology 120:331–339

Goodman SM, Langrand O (1996) A high mountain population of the ring-tailed lemur *Lemur catta* on the Andringitra Massif, Madagascar. Oryx 30:259–268

Graham TL, Matthews HD, Turner SE (2016) A global-scale evaluation of primate exposure and vulnerability to climate change. Int J Primatol 37:158–174

Grueter CC, Li D, Ren B, Li M (2013) Substrate use and postural behavior in free-ranging snub-nosed monkeys (*Rhinopithecus bieti*) in Yunnan. Integr Zool 8:335–345

Guo ST, Hou R, Garber PA, Raubenheimer D, Righini N, Ji WH, Jay O, He SJ, Wu F, Li FF, Li BG (2018) Nutrient-specific compensation for seasonal cold stress in a free-ranging temperate colobine monkey. Funct Ecol 32:2170–2180

Hanya G (2004) Seasonal variations in the activity budget of Japanese macaques in the coniferous forest of Yakushima: effects of food and temperature. Am J Primatol 63:165–177

Hanya G, Kiyono M, Hayaishi S (2007) Behavioral thermoregulation of wild Japanese macaques: comparisons between two subpopulations. Am J Primatol 69:802–815

Hanya G, Otani Y, Hongo S, Honda T, Okamura H, Higo Y (2018) Activity of wild Japanese macaques in Yakushima revealed by camera trapping: patterns with respect to season, daily period and rainfall. PLoS One 13:e0190631

Heldmaier G, Steinlechner S, Ruf T, Wiesinger H, Klingenspor M (1989) Photoperiod and thermoregulation in vertebrates: body temperature rhythms and thermogenic acclimation. J Biol Rhythms 4:139–153

Hill RA (2006) Thermal constraints on activity scheduling and habitat choice in baboons. Am J Phys Anthropol 129:242–249

Hill RA, Weingrill T, Barrett L, Henzi SP (2004) Indices of environmental temperatures for primates in open habitats. Primates 45:7–13

Ioannou S, Chotard H, Davila-Ross M (2015) No strings attached: physiological monitoring of rhesus monkeys (*Macaca mulatta*) with thermal imaging. Front Behav Neurosci 9:160

Janson C, Verdolin J (2005) Seasonally of primate births in relation to climate. Seasonality in primates: studies of living and extinct human and non-human primates. In: Brockman DK, Schaik CP (eds) Seasonality in primates: studies of living and extinct human and non-human primates. Cambridge University Press, Cambridge, pp 307–350

Kamilar JM, Muldoon KM (2010) The climatic niche diversity of Malagasy primates: a phylogenetic perspective. PLoS One 5:e11073

Kelley EA, Jablonski NG, Chaplin G, Sussman RW, Kamilar JM (2016) Behavioral thermoregulation in *Lemur catta*: the significance of sunning and huddling behaviors. Am J Primatol 78:745–754

Kobbe S, Nowack J, Dausmann KH (2014) Torpor is not the only option: seasonal variations of the thermoneutral zone in a small primate. J Comp Physiol B 184:789–797

Korstjens AH, Lehmann J, Dunbar RI (2010) Resting time as an ecological constraint on primate biogeography. Anim Behav 79:361–374

Kumar A, Singh M, Molur S (2008) *Macaca silenus*. The IUCN Red List of Threatened Species 2008. https://www.iucnredlist.org/. Accessed 18 Nov 2019

Kurup GU, Kumar A (1993) Time budget and activity patterns of the lion-tailed macaque (*Macaca silenus*). Int J Primatol 14:27–39

Lambert JE (1998) Primate digestion: interactions among anatomy, physiology, and feeding ecology. Evol Anthropol 7:8–20

Lhota S, Sha CM, Bernard H, Matsuda I (2019) Proboscis monkey conservation: beyond the science. In: Behie AM, Teichroeb JA, Malone N (eds) Primate conservation in the anthropocene. Cambridge University Press, Cambridge, pp 182–196

Li D, Ren B, Grueter CC, Li B, Li M (2010) Nocturnal sleeping habits of the Yunnan snub-nosed monkey in Xiangguqing, China. Am J Primatol 72:1092–1099

Lippold LK (1989) Reproduction and survivorship in Douc langurs *Pygathrix nemaeus* in zoos. Int Zoo Yearbook 28:252–255

Litchfield C, Dorrian J, Davis J, Lushington K, Dawson D (2011) Lessons in primate heat tolerance: a commentary based on the "Human Zoo" experience. J Appl Anim Welfare Sci 14:162–169

Lubbe A, Hetem RS, McFarland R, Barrett L, Henzi PS, Mitchell D, Meyer LC, Maloney SK, Fuller A (2014) Thermoregulatory plasticity in free-ranging vervet monkeys, *Chlorocebus pygerythrus*. J Comp Physiol B 184:799–809

Majolo B, McFarland R, Young C, Qarro M (2013) The effect of climatic factors on the activity budgets of a temperate primate, the Barbary macaque (*Macaca sylvanus*). Int J Primatol 34:500–514

McFarland R, Majolo B (2013) Coping with the cold: predictors of survival in wild Barbary macaques *Macaca sylvanus*. Biol Let 9:20130428

McFarland R, Barrett L, Boner R, Freeman NJ, Henzi SP (2014) Behavioral flexibility of vervet monkeys in response to climatic and social variability. Am J Phys Anthropol 154:357–364

McFarland R, Fuller A, Hetem RS, Mitchell D, Maloney SK, Henzi SP, Barrett L (2015) Social integration confers thermal benefits in a gregarious primate. J Anim Ecol 84:871–878

Mendiratta U, Kumar A, Mishra C, Sinha A (2009) Winter ecology of the Arunachal macaque *Macaca munzala* in Pangchen Valley, western Arunachal Pradesh, northeastern India. Am J Primatol 71:939–947

Milton K (1998) Physiological ecology of howlers (*Alouatta*): energetic and digestive considerations and comparison with the Colobinae. Int J Primatol 19:513–548

Morland HS (1993) Seasonal behavioral variation and its relationships to thermoregulation in ruffed lemurs. In: Ganzhorn JU, Kappeler PM (eds) Lemur social systems and their ecological basis. Plenum, New York, pp 193–205

Mutschler T (2002) Alaotran gentle lemur: some aspects of its behavioral ecology. Evol Anthropol 11:101–104

Nüchel J, Bøcher PK, Xiao W, Zhu AX, Svenning JC (2018) Snub-nosed monkeys (*Rhinopithecus*): potential distribution and its implication for conservation. Biodivers Conserv 1:1–22

Ostner J, Kappeler PM (2004) Male life history and the unusual adult sex ratios of redfronted lemur, *Eulemur fulvus rufus*, groups. Anim Behav 67:249–259

Paterson JD (1981) Postural-positional thermoregulatory behaviour and ecological factors in primates. Can Rev Phys Anthropol 3:3–11

Pochron ST (2000) Sun avoidance in the yellow baboons (*Papio cynocephalus cynocephalus*) of Ruaha National Park, Tanzania. Variations with season, behavior and weather. Int J Biometeorol 44:141–147

Pontzer H, Raichlen DA, Gordon AD, Schroepfer-Walker KK, Hare B, O'Neill MC, Muldoon KM, Dunsworth HM, Wood BM, Isler K, Burkart J (2014) Primate energy expenditure and life history. Proc Natl Acad Sci 111:1433–1437

Randall D, Burggren W, French K (1997) Eckert animal physiology: mechanisms and adaptations, 4th edn. Freeman, New York

Reed KE, Fleagle JG (1995) Geographic and climatic control of primate diversity. Proc Natl Acad Sci 92:7874–7876

Rothman JM, Bryer MA (2019) The effects of humans on the primate nutritional landscape. In: Behie AM, Teichroeb JA, Malone N (eds) Primate conservation in the anthropocene. Cambridge University Press, Cambridge, pp 199–215

Rothman JM, Chapman CA, Struhsaker TT, Raubenheimer D, Twinomugisha D, Waterman PG (2015) Long-term declines in nutritional quality of tropical leaves. Ecology 96:873–878

Satinoff E (2011) Behavioral thermoregulation in the cold. Compr Physiol 14:481–505

Schmid J, Speakman JR (2000) Daily energy expenditure of the grey mouse lemur (*Microcebus murinus*): a small primate that uses torpor. J Comp Physiol B 170:633–641

Sha JCM, Kurihara Y, Tsuji Y, Take M, He T, Kaneko A, Suda-Hashimoto N, Morimoto M, Takayoshi N, Zahariev A, Blanc S, Hanya G (2018) Seasonal variation of energy expenditure in Japanese macaques (*Macaca fuscata*). J Therm Biol 76:139–146

Silk JB (1994) Social relationships of male bonnet macaques: male bonding in a matrilineal society. Behaviour 130:271–291

Sussman RW (1991) Demography and social organization of free-ranging *Lemur catta* in the Beza Mahafaly Reserve, Madagascar. Am J Phys Anthropol 84:43–58

Struhsaker T, Oates JF, Hart J, Butynski TM (2008) *Cercopithecus neglectus*. The IUCN Red List of Threatened Species 2008. Accessed 21 Nov 2019

Tattersall GJ, Cadena V (2010) Insights into animal temperature adaptations revealed through thermal imaging. Imaging Sci J 58:261–268

Terrien J, Perret M, Aujard F (2011) Behavioral thermoregulation in mammals: a review. Front Biosci 16:1428–1444

Thierry B, Bynum EL, Baker S, Matsumura S, Muroyama Y, Brien TGO, Petit O, Watanabe K (2000) The social repertoire of Sulawesi macaques. Primate Res 16:203–226

Thompson CL, Powell BL, Williams SH, Hanya G, Glander KE, Vinyard CJ (2017) Thyroid hormone fluctuations indicate a thermoregulatory function in both a tropical (*Alouatta palliata*) and seasonally cold-habitat (*Macaca fuscata*) primate. Am J Primatol 79:e22714

Tsuji Y (2010) Regional, temporal, and interindividual variation in the feeding ecology of Japanese macaques. In: Nakagawa N, Nakamichi M, Sugiura H (eds) The Japanese macaques. Springer, Japan, pp 99–127

Troisi A, Schino G (1986) Diurnal and climatic influences on allogrooming behaviour in a captive group of Java monkeys. Anim Behav 34:1420–1426

Van Doorn AC, O'riain MJ, Swedell L (2010) The effects of extreme seasonality of climate and day length on the activity budget and diet of semi-commensal chacma baboons (*Papio ursinus*) in the Cape Peninsula of South Africa. Am J Primatol 72:104–112

Van Schaik CP (2013) The costs and benefits of flexibility as an expression of behavioural plasticity: a primate perspective. Philos Trans R Soc B Biol Sci 368:20120339

Van Schaik CP, Brockman DK (2005) Seasonality in primate ecology, reproduction and life history: an overview. In: Brockman DK, Schaik CP (eds) Seasonality in primates: studies of living and extinct human and non-human primates. Cambridge University Press, Cambridge, pp 3–20

Walker FM, Sajita NK (2011) Long-term persistence of de Brazza's Monkey (*Cercopithecus neglectus*) in a Kenyan Forest fragment. J East Afr Nat Hist 100:69–87

Weingrill T, Gray DA, Barrett L, Henzi SP (2004) Fecal cortisol levels in free-ranging female chacma baboons: relationship to dominance, reproductive state and environmental factors. Horm Behav 45:259–269

Yang J, Liu HZ, Ou CQ, Lin GZ, Zhou Q, Shen GC, Chen PY, Guo Y (2013) Global climate change: impact of diurnal temperature range on mortality in Guangzhou, China. Environ Pollut 175:131–136

Yanuar A, Chivers DJ, Sugardjito J, Martyr DJ, Holden JT (2009) The population distribution of pig-tailed macaque (*Macaca nemestrina*) and long-tailed macaque (*Macaca fascicularis*) in west central Sumatra, Indonesia. Asian Primates J 1:2–11

Zhao X, Ren B, Li D, Garber PA, Zhu P, Xiang Z, Grueter CC, Liu Z, Li M (2019) Climate change, grazing, and collecting accelerate habitat contraction in an endangered primate. Biol Cons 231:88–97