Behavioral flexibility of vervet monkeys in response to climatic and social variability

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Abstract

Responses to environmental variability sheds light on how individuals are able to survive in a particular habitat and provides an indication of the scope and limits of its niche. To understand whether climate has a direct impact on activity, and determine whether vervet monkeys have the behavioral flexibility to respond to environmental change, we examined whether the amount of time spent resting and feeding in the non-mating and mating seasons were predicted by the thermal and energetic constraints of ambient temperature. Our results show that high temperatures during the non-mating season were associated with an increase in time spent resting, at the expense of feeding. Cold temperatures during the non-mating season were associated with an increase in time spent feeding, at the expense of resting. In contrast, both feeding and resting time during the mating season were independent of temperature, suggesting that animals were not adjusting their activity in relation to temperature during this period. Our data indicate that climate has a direct effect on animal activity, and that animals may be thermally and energetically compromised in the mating season. Our study animals appear to have the behavioral flexibility to tolerate current environmental variability. However, future climate change scenarios predict that the time an animal has available for behaviors critical for survival will be constrained by temperature. Further investigations, aimed at determining the degree of behavioral and physiological flexibility displayed by primates, are needed if we are to fully understand the consequences of environmental change on their distribution and survival.

The trade-offs involved in balancing energy and time budgets have long been a focus of behavioral research. Among primates, the constraints imposed by intense sociality add an extra layer of complexity, as animals must trade off the benefits of group living (e.g., protection from predators) against the costs of competing within these groups for resources. Animals must also make compromises between different activities, such as feeding, resting socializing and moving, that reflect the attempt to maintain a positive energy balance while remaining coordinated with their conspecifics. In many cases, the trade-offs between different maintenance activities have been shown to reflect differences in resource abundance and quality, which dictates the amount of time that must be devoted to feeding, which then necessarily limits the amount of time available for other activities (Dunbar et al., 2009). In particular, the ability to engage socially with others has been shown to have consequences for both long- and short-term survival (Silk et al., 2009, 2010; Schülke et al., 2010; McFarland and Majolo, 2013). Social behaviors like grooming may also play a role in maintaining group cohesion over time, whereas a lack of social maintenance may result in groups becoming destabilized, leading to group fission (Henzi et al., 1997) and the potential loss of sociality benefits. Time available to rest has often been considered simply as a ‘reserve’ of time left over after other essential activities have been fulfilled (Dunbar, 1992). More recently, two separate forms of resting have been identified (e.g., Dunbar et al., 2009): ‘free’ resting time, defined as a reserve of time that can be converted into additional feeding, moving or socializing, and ‘enforced’ resting time, defined as the time required for thermoregulation and digestion. Due to the importance of thermoregulation and digestion, constraints on available resting time may have consequences for a species’ ability to exist in particular habitats (Korstjens et al., 2010).

Given potential thermoregulatory constraints, it is clear that climate, namely ambient temperature and rainfall, may pose a very direct constraint on activity, in addition to its impact on the quality and distribution of available food resources (e.g., Del Grosso et al., 2008), and hence the amount of time an animal needs to spend feeding to fulfill its energetic requirements. The "thermoneutral zone" is defined as the range of environmental temperatures within which an animal's metabolic rate and evaporative heat loss is minimal (Gordon, 1985). For primates, the thermoneutral zone is approximately 25 to 30°C (Elizondo, 1977). The maintenance of homeothermy in primates involves a combination of both autonomic and behavioural processes, where behavioural changes should be used first as a means to conserve the water and energy required for autonomic processes.

To date, the impact of direct climatic constraints on activity budgets has received little attention. We do know that, at high temperatures, some studies have revealed that animals tend to spend more time resting (Stelzner, 1988; Hill, 2006; Campos and Fedigan, 2009; Korstjens et al., 2010; Sato, 2012; Majolo et al., 2013), and that resting and shade-seeking are critical for thermoregulation (e.g., Campos and Fedigan, 2009): high heat load can cause severe dehydration and potentially fatal hyperthermia (Taylor, 1970). In contrast to the reduced demand for shade-seeking and resting in colder temperatures, the energetic demands of thermoregulation and digestion are higher in cold conditions (Satinoff, 2011), meaning more time needs to be spent feeding (Satinoff, 2011; Majolo et al., 2013)

The majority of social primates need to spend time maintaining their grooming relationships with conspecifics, which is also likely to detract from their time available to feed and rest. Other forms of social demand, such as mating, may also constrain activity, especially among seasonal breeders where mating effort is concentrated into a short period. Among these species, males in particular can spend significant amounts of time competing for and mate-guarding females (Henzi and Lucas, 1980; Muller and Wrangham, 2009). If this occurs at the expense of feeding and resting, it may cause them to become thermally and energetically compromised. Females may also be compromised due to time constraints imposed on them by male socio-sexual behavior.

Future climate change scenarios predict that, over the next 100 years, South Africa will be exposed to increased aridity and higher annual temperatures (Midgley et al., 2001). This in turn is expected to have a significant impact on species survival and distribution (Erasmus et al., 2002; Hoffman et al., 2009; Korstjens et al., 2010). Here, we explore direct climatic effects on the on activity of wild vervet monkeys (*Chlorocebus pygerythrus*), during both the non-mating and mating seasons, as a means of assessing how animals prioritize behavior and whether they possess sufficient behavioral flexibility to adjust their activity budget in response to competing demands. As we will show, this investigation is particularly relevant to vervet monkeys living below the equator, in a semi-desert habitat, as they experience a highly variable seasonal climate. Given that (i) our study population in the semi-arid Karoo is at the most southerly limits of the vervet distribution and (ii) is a challenging habitat for such a water-dependent species (McDougall et al., 2010), it becomes pertinent to assess the scope and limits of their behavioral flexibility in response to current climatic fluctuations.

During the non-mating season, we predicted that (i) higher ambient temperatures would be associated with increased resting time, in order to reduce heat load and water loss, whereas feeding would be prioritized at cold temperatures to fulfill the increased energetic demands of thermoregulation. During the mating season, we predicted that (ii) both males and females would become thermally and energetically compromised compared to the non-mating season because of the additional time-constraints imposed by socio-sexual behavior. We therefore predicted that (iii) time spent resting and feeding by each sex would be unresponsive to temperature during this period. In all our analyses, we controlled for the effects of estimated food abundance and group size on activity patterns, allowing us to test the relative importance of climatic and ecological factors on activity patterns. That is, we took into account the fact that, when food abundance is low and group size is larger, more time is expected to be spent searching for food due to increased feeding competition (i.e. rates of aggression and patch depletion: Janson, 1988; Isbell 1991) and that, when group sizes are larger, more time is expected to be spent socializing as more social relationships need to be managed to maintain group cohesion (Dunbar, 1991; Lehmann et al., 2007).

METHODS

Data were collected between January 2009 and March 2013 from two groups (named RBM and RST) of wild vervet monkey living on the Samara Private Game Reserve in the Karoo, Eastern Cape, South Africa (32°22'S, 24°52'E). Our study region is characterized as semi-arid riparian woodland, where our study animals feed predominantly on seeds, flowers, leaves, berries, gums and insects. For more details of their diet, see Pasternak et al. (2013). Vervet monkeys live in multi-male, multi-female societies (e.g., Isbell et al., 1991). Females are philopatric and males tend to emigrate from their natal group at the onset of puberty. Vervet monkeys are seasonal breeders and increased rates of male migration are typically observed at the onset of the mating season (Henzi and Lucas, 1980). During the mating season, males compete for access to mating opportunities with females.

Data were collected from all adult (males ≥ 6 years; females ≥ 4 years) and sub-adult (males = 4 to 5 years; females = 3 to 4 years) group members. Over the entire study period, the average group sizes of RBM and RST were 26 and 36 adult and sub-adult animals, respectively. Relatively small yearly changes in average group size were observed (ranges: RBM = 23 to 30; RST = 34 to 38; mean rate of change: RBM and RST = ±3 animals/year) suggesting that normal growth cycles (i.e., maturation of juveniles) and inter-birth intervals were consistent across the study period. A larger degree of monthly variability in group sizes (ranges: RBM = 17 to 36; RST = 31 to 44) was likely the result of fluctuations in rates of male migration. The mating season in this region typically falls between April and June, while the birth season typically falls between November and January. The hottest and wettest time of the year is from November to March and the coldest and driest time of the year occurs between June and August. All study animals were habituated to the presence of human observers, were individually recognizable, and lived on a completely natural diet (Pasternak et al., 2013). This study was entirely observational and did not affect the welfare of our study animals.

Instantaneous scan sampling methods (Altmann, 1974) were used to collect data on the activity time budgets of all adult and sub-adult group members from the two groups. Scan data were collected every thirty minutes from all individuals that could be located within a ten-minute time window. The activity of each subject was recorded as falling into one of five mutually exclusive categories: i) Resting: when an animal was stationary without feeding or socializing, ii) Feeding: when an animal was consuming food, iii) Moving: when an animal was moving without feeding, iv) Socializing: when an animal was involved in allo-grooming, v) Other: when an animal was involved in aggressive, mating or play behavior. Any given animal was sampled only once within each scan. Across the four year study period, a total of 50,591 and 61,381 scans were collected from RBM and RST, respectively. Group censuses were taken daily to provide information on group size.

Climate data for the entire study period were available from a local weather station (32°12’S, 24°33’E), which provided information on daily ambient temperatures (°C: mean, maximum and minimum), relative humidity (%) and rainfall (mm). Of the 865 days on which we collected behavioral data, climate data were unavailable for 158 days, leaving 707 days of observation as the focus of our analysis.

Seasonal patterns of the net primary productivity of plant biomass – across all climatic zones – have been shown to be positively correlated with rainfall (e.g., Del Grosso et al., 2008). Several studies specific to our study region (i.e., the Karoo, Eastern Cape) have also demonstrated positive correlations between vegetation abundance and rates of rainfall (e.g., Hoffman et al., 1990; du Toit, 2002). Therefore, because we did not directly collect food abundance data over the entire study period, we used rainfall as a proxy for monthly food abundance (e.g., Coe et al. 1976; Barton et al., 1992; Hill et al., 2003). Since there is a time-lag in the effect that rainfall has on vegetation biomass, and hence the abundance of food available, we used two-month cumulative rainfall as an estimate of food abundance (e.g., Barton et al., 1992).

Data analysis

We calculated, at the group level, the proportion of scans collected each day that our subjects spent resting, feeding, moving and socializing. This was calculated separately for males and females. We ran a series of generalized linear mixed models (GLMMs) to explore the effect of climatic variability on activity. The following analyses were repeated independently on males and females for both the non-mating and mating seasons. We entered either the proportion of time spent resting, feeding, socializing or moving as our dependent variables. We applied an arcsine transformation to all our dependent variables to improve normality. Our five climatic variables (mean, maximum and minimum ambient temperatures, rainfall and relative humidity) were all highly inter-correlated (all $P<0.001$), with the exception of minimum ambient temperature and relative humidity ($P=0.14$). Mean ambient temperature was positively correlated with maximum and minimum ambient temperatures and rainfall, and negatively correlated with relative humidity. Therefore, of our five climatic variables, we entered only mean daily ambient temperature as an independent variable into our model. Estimated monthly food abundance and group size were also entered as independent variables. We entered the number of daylight hours for each scan day, and the month of the year as control fixed factors in order to account for potential seasonal changes in activity patterns (e.g., Hill et al., 2003). We entered the day of the scan nested inside group ID as random factors to control for the non-independence and clustering of our dataset (Pinheiro and Bates, 2000; Tabachnick and Fidell, 2007). Scans were collected from both groups on the same day.

This 'full model' approach allowed us to explore the effect that our independent variables had on our dependent variables, whilst controlling for the effects of our control variables. For the sake of brevity, we discuss only those results directly related to our predictions. All analyses were performed in STATA v10 Software (StataCorp, 2007). See Tables 1 and 2 for details of the effects of temperature, estimated food abundance and group size on the four main activity categories (i.e., resting, feeding, socializing and moving). See the electronic supplementary material for full GLMM results (Tables S1 and S2).

RESULTS

Seasonal trends in climate and activity

Over the four-year study period, mean ambient temperatures ranged from -5.8 ˚C to 42.1˚C. The summer months (November to March) can be characterized as receiving higher ambient temperatures, rainfall and relative humidity compared to the winter months (June to August: Fig. 1). Both the non-mating and mating seasons showed large ranges in mean ambient temperature (non-mating season = 3.7˚C – 30.3˚C; mating season = 3.8˚C – 24.6˚C) and estimated food abundance (non-mating season = 0.25mm – 128.53mm; mating season = 7.36mm – 142.49mm). High and low temperatures were observed in both the non-mating (highest = 42°C, lowest = 0°C) and mating season (highest = 37°C, lowest = 0°C). The amount of time spent feeding was highly variable across the year (Fig. 2), ranging from approximately 20% of the day in the hot, wet summers, to over 40% of the day in the cold, dry winters. Conversely, the amount of time spent resting was highest in the summer (~45%), and lowest in the winter (~30%). The time spent moving or socializing was less variable, with time spent moving ranging between 20% and 30% of the day across the year, while time spent socializing consistently accounted for less than 10% of the day across the year. The seasonal patterns we observed in estimated food abundance, feeding time and stages of reproduction (Fig. 2), support the view that vervet monkeys synchronize their reproduction to make sure they have access to sufficient resources to succeed (Lee, 1987; Butynski, 1988).

The non-mating season

Insert Figs. 1 and 2

In support of our prediction, a significantly larger proportion of time was spent resting at higher temperatures, compared to lower temperatures for both males and females in the non-mating season (Table 1a). A significantly larger proportion of time was spent feeding in lower temperatures compared to higher temperatures for both males and females (Table 1b). The proportions of time spent feeding and moving were unrelated to estimated food abundance for both males and females (Tables 1b, d). Similarly, the proportion of time spent socializing was unrelated to the size of the group for both males and females (Table 1c).

The mating season

Insert Table 1

In support of our prediction, the proportion of time spent resting was unrelated to temperature for both males and females in the mating season (Table 2a). Similarly, the proportion of time spent feeding was unrelated to temperature for both males and females (Table 2b). For males, significantly larger proportions of time were spent feeding (Table 2b), and smaller proportions of time spent moving (Table 2d) when estimated food abundance was high. For females, although the proportion of time spent feeding was unrelated to estimated food abundance (Table 2b), they spent a significantly smaller proportion of time moving when estimated food abundance was high (Table 2d). In partial support of our prediction, males, but not females, spent a significantly larger proportion of time socializing when group sizes were larger (Table 2c).

Insert Table 2

DISCUSSION

Vervet monkeys in our study population spent more time resting when temperatures were high, and did so at the expense of feeding. When temperatures were cold, more time was spent feeding at the expense of resting. These findings are congruent with the suggestion that animals prioritize staying cool in hot periods to reduce heat load and water loss, and consume more food in cold periods to satisfy the increased energetic demands of thermoregulation and digestion.

Although it has been argued frequently that time spent resting is a ‘reserve’ of spare time that can easily be given over to feeding during periods of increased energetic demand, this fails to recognize the importance of resting time for behavioral thermoregulation. Although it has been suggested that, in baboons, resting and shade-use are used only opportunistically (Hill, 2006) – as the priority is presumed to always be feeding – our results indicate that, for vervet monkeys, the importance of resting is so strong that resting is prioritized over feeding at high temperatures. Potential differences between these two species in their ability to tolerate heat exposure might be explained by the smaller body mass of vervet monkey compared to baboons, which makes them more labile to changes in ambient temperature. Baboons, for example, have been shown to tolerate much higher heat loads than expected (Brain & Mitchell 1999; Mitchell et al. 2009).

In addition to the direct constraint that temperature has on activity, temperature also indirectly affects activity through its determination of habitat productivity and food abundance (e.g., Clutton-Brock, 1977; Wrangham, 1980). In our study, however, the direct impact of climate (i.e., mean ambient temperature, which was positively correlated with rainfall and negatively correlated with humidity) was the most influential factor in predicting the amount of time an individual had available to rest and feed. When controlling for the effect of ambient temperature, we found no evidence that estimated food abundance or the size of the group was related to the time spent feeding or resting. These findings are consistent with previous conclusions made on the importance of the thermal environment in predicting activity patterns in primates (e.g., Hill, 2006; Korstjens et al., 2010).

We found that, in the mating season, time spent resting and feeding was unrelated to temperature, suggesting that individuals were not adjusting their behavior to prioritize thermoregulatory and energetic efficiency. Instead, these results suggests that, due to the necessary investment in socio-sexual behavior and its associated reproductive benefits, both males and females were exposing themselves to higher heat loads than they would typically, and were feeding less than their energetic requirements demanded. In contrast to the non-mating season, estimated food abundance had a significant impact on activity in the mating season. Both males and females spent more time moving when estimated food abundance was low. This is congruent with the suggestion that individuals should be able to feed more, relative to the time they spend searching for food, when food abundance is high (Janson, 1988). Curiously however, this relationship was only observed in the mating season, not in the non-mating season. Our finding that climate constrains activity in the non-mating season, but not the mating season, may help us explain these results. In the non-mating season, feeding times were most strongly predicted by temperature, and were unrelated to estimated food abundance. However, in the mating season, when individuals appear to behave independently of climate (due to the importance of socio-sexual behavior), foraging behaviors (i.e., feeding and moving) are more strongly predicted by estimated food abundance. This may also be due to the exponential decline in estimated food abundance in the mating season (see Fig. 1), making animal activity more sensitive to food abundance during this period.

In contrast to the suggestion that group size is a major determinant of social behavior in primates (Dunbar, 1991), we found no relationship between the size of the group and the proportion of time spent socializing. Although the robustness of the relationship between grooming (the constituent of our social activity category) and group size, and its importance to group cohesion, has recently been questioned (Grueter et al., 2013; but see Dunbar and Lehmann, 2013), it is important to note that Dunbar's analyses were run at the level of the population and species (Dunbar, 1991), and so may not necessarily apply to these fine-grained differences within a given habitat and population. Alternatively, the absence of a relationship between group size and social time may be a reflection of the unusually large group sizes of vervet monkey observed during this study. As reviewed in Pasternak et al. (2013), the large size of our study groups compared is likely to reflect the particular nature of their habitat: our study groups occupy high quality riparian habitat, which is surrounded by low quality habitat with a lack of water. This leads to a high density of vervet groups along the river system, and seems to retard fission into smaller groups (as this would require daughter groups to occupy the low quality areas beyond the river). Lehmann et al. (2007) suggested that when primate group sizes are over 40, ecological pressures are more likely to compromise the time available individuals have to groom. Our findings support this view.

In the mating season males, but not females, spent more time being social when group sizes were larger. Although these findings fit with the hypothesis that larger group sizes require more time to be devoted to grooming to enhance group cohesion (Dunbar, 1991), the fact that this relationship was observed only in the mating season, and only in males, suggests that the increase in grooming behavior is more likely a result of the increased prevalence of mating. In the mating season males tend to spend more time grooming females to improve mating opportunities (Gumert, 2007). Moreover, due to the higher frequencies of male-male competition in the mating season (Henzi and Lucas, 1980) – where dominant individuals tend to gain better access to females (Cowlishaw and Dunbar, 1991; Majolo et al., 2012) – grooming is likely to play an important role in managing male-male conflict. For example, grooming is often exchanged by former opponents to reconcile the costs of aggression (Cheney and Seyfarth, 1989; McFarland and Majolo, 2011a,b). Therefore, when group sizes are larger in the mating season – in terms of both potential mating partners and competitors – there is likely to be increased demand for social activity. The difficulty of monopolizing females in larger groups in the mating season (Cowlishaw and Dunbar, 1991) may also explain why females were able to spend more time feeding when group sizes were larger; as their activity was less constrained by male socio-sexual behavior. Concomitantly, animals would need to spend more time feeding when group sizes were larger due to overall increased rates of feeding competition (Henzi et al., 2013).

Taken together, our findings support the view that climate has a direct and significant impact on animal activity patterns. Climate clearly constrains the activity of vervet monkeys, and our results suggest that, at least within this region of their geographic distribution, they have the behavioral flexibility to respond to variability in temperature in order to fulfill their thermal and energetic demands. However, during the mating season both males and females potentially appear to be thermally and energetically compromised, due to the increased demand and importance of socio-sexual behavior. Future studies need to explore in more detail how the mating season affects physiological condition. A number of recent studies have contributed our understanding of the cortisol stress response of primates during such periods (e.g., Ostner et al., 2008; Higham et al., 2012; McFarland et al., 2013). Future important avenues of research should include the assessment of body temperature patterns and body condition in response to environmental stress. Such data will provide an indication of the thermoregulatory efficiency of a species or population, and assess whether they have the ability to maintain homeothermy when stressed.

The current thriving distribution of vervet monkeys in the Eastern Cape (Pasternak et al., 2013) indicates that our study animals' current environmental variability is within a range that they are able to tolerate. However, climate change scenarios predict that the Karoo will get increasingly hot and dry over the next 100 years (Midgley et al., 2001), which could affect species distribution, threatening their survival (Erasmus et al., 2002; Hoffman et al., 2009; Korstjens et al., 2010). Korstjens et al. (2010) propose that a 2°C increase in ambient temperature will demand an increase in 'enforced' resting time (i.e., for thermoregulation) which will significantly constrain the time available for other important behaviors such as feeding and socializing. Further investigation into whether a species has the physiological (including behavioral) flexibility to deal with environmental stress – in terms of extreme heat and cold, drought, food shortages and loss of favorable microclimates – are urgently needed if we are to fully understand the consequences that a changing environment will have on its distribution and survival.

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FIGURE LEGENDS

Fig. 1 Mean monthly ambient temperatures (mean, maximum and minimum), relative humidity and rainfall across the entire study period (January 2009 – March 2013)

Fig. 2 Seasonal patterns of (a) male and (b) female feeding and resting time in relation to estimated food abundance, ambient temperature and phase of reproduction