The effect of climatic factors on the activity budgets of the Barbary macaque (*Macaca sylvanus*)

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Abstract

Climatic conditions can significantly affect the behaviour of animals and constrain their activity or geographic distribution. The Barbary macaque (*Macaca sylvanus*) is one of the few primates that live outside the tropics. Here we analyse if and how the activity budgets of the Barbary macaque are affected by climatic variables (i.e. air temperature, relative humidity, rainfall, and snow coverage). We collected scan sampling data, over a period of almost three years, on the activity budgets of four groups of macaques living in the Middle Atlas Mountains of Morocco. This habitat is characterized by extreme seasonal changes, from cold and snowy winters, to hot and dry summers. The activity budgets of the macaques differed across months but not across the time of day (with the exception of time spent feeding). The monkeys spent significantly more time feeding or foraging when there was no snow than when snow coverage was moderate or major. Daily rainfall was positively related to resting time and negatively to time spent moving or in social behaviour. Air temperature was negatively related to time spent feeding or foraging. Finally, time spent on social behaviour was significantly lower when relative humidity was high. These data indicate that environmental factors significantly affect the time budgets of the endangered Barbary macaque, a species that has been little studied in the wild. Our study is one of the first accounts of how a temperate primate responds to climatic variables.

Keywords: climate, feeding, Morocco, resting, thermo-regulation

Introduction

Climatic factors, such as air temperature and rainfall, are known to affect the population density, habitat selection, group size and reproductive success of non-human primates (e.g. Bernstein 1972; Iwamoto and Dunbar 1983; Stelzner, 1988; Isbell and Young 1993; Ostner 2002; Ventura et al. 2005; Hill 2006). Moreover, climatic factors can constrain the activity budgets of an animal (Dunbar 1992; Dunbar et al. 2009). In order to maintain homeothermy (the ability of an organism to maintain a core body temperature within a narrow range when subjected to a wide range of environmental temperatures) animals may change their behaviour to keep their body warm or cold. This can be achieved, for example, by changing posture (huddling, sun-basking), selecting appropriate microclimates or prioritising the amount of time spent being active or inactive (e.g. Barrett et al. 2004; Campos and Fedigan, 2009; Hetem et al. 2012; Sato 2012). However, behavioural thermoregulation can be a costly activity in terms of time and energy, often taking place at the expense of other critical behaviours for survival (e.g. feeding, drinking and social activity; Hill et al. 2004; Hill 2006). For example, resting time increases in baboons (*Papio* spp.) when air temperature is high but such an increase is constrained by the time required to feed (Dunbar 1992; Hill 2006; Korstjens et al. 2010). In habitats where air temperature reaches levels that force baboons to increase resting time to a point which constrains feeding and prevents animals from reaching their daily energetic requirements, baboons cannot survive unless they use alternative feeding tactics (e.g. prolonged feeding at dawn and dusk; Hill 2006). Responses to climatic conditions are expected to be particularly pronounced in primate species living in habitats where the climate can vary dramatically during the day or across seasons. For example, black and white snub-nosed monkeys (*Rhinopithecus* *bieti*) make extensive use of fallback food (e.g. bark) during the cold winter months (Xiang et al. 2007). A similar feeding strategy is used by the Barbary macaque (*Macaca sylvanus*) in the hot summer months when bark becomes an important source of water and nutrients (Ménard and Qarro 1999).

Together with its importance for activity budgets and feeding ecology, understanding how primates respond to climatic variables also has important implications for conservation biology. The magnitude of the constraint that climatic variables, time, and diet impose on behaviour in a range of primate species determines their geographic distribution (Isbell and Young 1993; Hill et al. 2003; Dunbar et al. 2009; Korstjens et al. 2010). Therefore, data on diet and climatic variables can be used to model the extinction risk of a species or population and to select suitable areas for re-introduction programs (Dunbar et al. 2009; Korstjens et al. 2010). For example, such models have predicted that the distribution of African colobines is constrained by high temperature and that populations could collapse if annual temperature increased by 2ºC (Dunbar et al. 2009). These models view areas with low temperature (e.g. mountain ranges) as excellent habitats for colobines. However, we need empirical data on how these species cope with cold climate to make reliable inferences on whether such areas can indeed sustain a viable population of colobines. These recent studies on African colobines (Dunbar et al. 2009; Korstjens et al. 2010) highlight the importance of analysing the link between climatic conditions and behaviour, particularly in threatened species or those that live at the boundaries of the geographic distribution of primates (i.e. outside the tropics, at high altitudes, or in dry/cold climates; Fleagle 1999).

The Barbary macaque is one of the few primate species living outside the tropics, inhabiting the mountainous parts of Morocco and Algeria (Ménard, 2002), at an elevation of between 400 and 2,300 meters above sea level (Mehlman 1989; Fooden 2007). Barbary macaques experience extreme and diverse climatic conditions across seasons, from cold and snowy winter months to dry and hot summers (Ménard and Vallet 1997; Ménard 2002). This species is listed as endangered (IUCN 2012) and its population has decreased dramatically over the last few years (current estimate is between 5,000 and 10,000 individuals; van Lavieren and Wich 2009) due to habitat destruction and human disturbance. The current distribution of the Barbary macaque may not reflect their preferred habitat, but rather the region in which they have been restricted to due to competition for land with humans (Fa 1984), which has increased steadily over the last two thousand years (Taub 1984). According to this hypothesis, human activity has restricted the distribution of Barbary macaques to mountainous areas, away from the previously inhabited lower altitude habitats and milder climates (e.g. plains and coasts: Fa 1984; Camperio Ciani et al. 2005; Waters et al. 2007).

Notwithstanding the threats and ecological pressure faced by the Barbary macaque, research on the ecology of this species in the wild is relatively scarce and patchy. For example, we know that the activity budgets of Barbary macaques show marked seasonality (Ménard and Vallet 1997) and differ significantly between wild and provisioned groups (el Alami et al. 2012). However, no study has so far directly investigated the effect that climatic conditions can have on the behaviour of this species. Our aim was to determine if and how climatic factors (i.e. air temperature, relative humidity, rainfall, and snow coverage) affect the activity budget of the Barbary macaque. Addressing this topic is important as a better understanding of the behavioural ecology of this species is essential to protect the Barbary macaque in the wild. For example, if the macaques struggle to cope with the cold winters of the Atlas Mountains an effort should be made to create protected areas for the monkeys at lower altitudes. Moreover, research on species living at the climatic extremes of primate distribution can shed light on what ecological barriers restrict primate species to their current geographic distribution.

Based on the marked seasonal climatic differences of the Middle Atlas Mountains and on the seasonality of the behaviour of Barbary macaques (Ménard and Vallet 1997), we expect climatic factors to have a significant effect on the activity budgets of this study population. For example, we expect snow coverage to have a significant impact on the feeding ecology of this species (similar to Japanese macaques, *Macaca fuscata*; Nakayama et al. 1999), as Barbary macaques often forage on the ground (Ménard and Vallet 1997; Menard 2002).

Methods

Study site and subjects

The field site where we conducted this study is between 1,500 and 2,050 meters above sea level and is mainly composed of an indigenous oak and cedar forest (*Cedrus atlantica* & *Quercus ilex*). Jackals (*Canis aureus*), genets (*Genetta genetta*), domestic dogs (*Canis lupus familiaris*), and several species of birds of prey inhabit the area and are potential predators of the macaques. Barbary macaques are a diurnal species (Deag 1985) and their diet consists largely of leaves, seeds and grass (Ménard 2002; el Alami et al. 2012).

Subjects of this study were all adult and sub-adult monkeys from four groups (i.e. Flat-face, Large, Scarlet and Green group; Table 1) of wild Barbary macaque living in the Middle Atlas Mountains, Morocco (33° 24’N – 005° 12’W). See the Data analysis section below for a discussion on how we controlled for study group differences in our analyses. The study groups were fully habituated to researchers and were not provisioned by humans. Three of the study groups (Flat-face, Large and Scarlet group) inhabited the same forest patch and their home ranges were partially over-lapping (average home-range over-lapping: 35%), whereas the Green group inhabited a different forest patch approximately 18 Km away. We collected data on home range overlap via a Garmin eTrex GPS device (© Garmin, U.S.A.) immediately before the start of a scan sample (see below), during the whole course of this study.

The Haut Commissariat aux Eaux et Forêts et à la Lutte Contre la Désertification of Morocco provided research permission. This study was entirely observational and did not affect the welfare of our study animals; it complied with protocols approved by the Ethics Committee of the University of Lincoln and adhered to the legal requirements of Germany, Morocco and the U.K.

Data collection

We collected data between June 2008 and January 2011 during full-day follows conducted across different time periods for each of the four groups (Table 1). We could not collect any data between mid-December 2008 and mid-January 2009 due to closure of the road leading to the field-site following exceptionally high snowfall. After returning to the field in January 2009, we noticed that 36 monkeys were missing from the Flat-face and Large groups (Table 1). In spring 2009 we surveyed the forest patch inhabited by the two groups to determine if the missing monkeys had emigrated to neighbouring groups. We found that only five of the 36 missing monkeys had joined neighbouring groups. However, we found the remains of seven monkeys in the home ranges of our two study groups. Therefore, it is likely that the majority of the missing individuals did not survive the harsh 2008 – 2009 winter. The composition and size of the Scarlet and Green groups remained stable over the data collection periods.

RM and CY collected data daily between 0700 and 1800hrs, with the help of eight research assistants, using a Pocket PC loaded with Pendragon Forms Version 5.1 (© Pendragon Software Cooperation, U.S.A.). We used scan sampling to collect data on the activities of the study animals (Table 1). We collected scan samples (Altmann 1974) every hour (at 0700, 0800, and so on until 1800hrs). Every month, we conducted parallel observations to check for inter-observer reliability. Comparison of these parallel scan sampling data showed that inter-observer agreement was always above 95%. We collected scan data on the largest possible number of study animals observed within a ten minute period. In each scan sample we recorded data on six mutually-exclusive activities: 1) Feeding (defined as a monkey picking up food or gnawing); 2) Foraging (a monkey searching for food and/or processing food without eating it); 3) Moving (a monkey moving on the ground climbing on a tree/rock while not foraging); 4) Resting (a monkey sitting still while not engaged in any of the other activities listed here, or sleeping alone or in physical contact with another individual); 5) Social (a monkey engaged in a grooming interaction, in social play, in a triadic-buffering interaction (Deag 1980) or teeth chattering); 6) Other (included vigilance, mating, aggression or non-social play with an object).

At the beginning of each scan, we recorded air temperature and relative humidity using a 3500 Kestrel Pocket Weather Station (© Kestrel Meters, U.S.A.). We placed the weather station in the shade at 1.5 meters above the ground. We recorded elevation above sea level using a Garmin eTrex GPS device. At the end of each observation day we recorded daily rainfall using two TFA rain-gauges (© TFA, Germany) placed at two locations (respectively, at the centre of the forest patch inhabited by the Flat-Face, Large and Scarlet groups and of the forest patch inhabited by the Green group). For each observation day, we defined snow coverage in a group's home range according to three categories: 1) no snow; 2) moderate snow coverage (between 1 and 49% of the area); 3) major snow coverage (i.e. between 50 and 100% of the area). We did not collect data on the depth of snow coverage as snow melted at different rates in the home range (depending on exposure of a given area to sunlight/shade). Therefore, we could not record an accurate measure of snow depth. Note that the results presented below significantly under-estimate the actual days of snow coverage faced by the monkeys (especially days of major snow coverage), as during days of heavy snow the road leading to the field site was often closed.

Data analysis

We ran the analyses presented here using 3,404 scan samples collected during 641 days. The activities listed above were our dependent variables in a series of linear mixed models (LMM; Tabachnick and Fidell 2007). We did not include the percentage of time the monkeys spent in the Other activity (see above) in the analyses presented below as it comprised less than 5% (mean ± SE = 4.33 ± 0.70%) of the activity budget of the study animals. To analyse the effect of climatic variables on activity budgets we entered, as fixed factors, the following four variables into the LMMs: 1) Snow coverage (using the three categories described above); 2) Daily rainfall (in millimetres); 3) Air temperature (ºC); 4) Relative humidity (expressed as a percentage). We entered the four variables together in the LMMs, as this procedure allowed us to test the relative importance of each climatic variable (e.g. the effect of air temperature on feeding while controlling for snow coverage, daily rainfall and relative humidity). In the LMMs we also entered, as control fixed factors, the month of the scan and time of day of each scan (e.g. 0700, 0800 and 0900hrs) to control for daily and seasonal effects. This method allowed us to differentiate the proximate effect of climate on activity budgets from the effect of seasonality and circadian rhythm. Elevation above sea level (in metres) had no significant effect on activity budget (average P values from the LMMs run on each activity = 0.76). We thus excluded this variable from the analyses presented below. Finally, in the LMMs we entered, as random factors, day of the scan nested into Group ID. This procedure controlled for the non-independence and clustering of data as multiple scans were collected across each observation day from the same group (Pinheiro and Bates 2000; Tabachnick and Fidell 2007). Moreover, this procedure allowed us to analyse the effect of climatic variables on activity budgets while controlling for differences in group size of our study groups (because our aim here was not to test the effect of group size differences on activity budgets). Due to their large change of group size during the 2008-2009 winter (see above and Table 1), we split both the Flat-face and Large groups in two separate categories (before and after the group size change). Therefore, we had six categories for the Group ID variable (i.e. Flat-face before, Flat-face after, Large before', Large after, Scarlet, and Green). We transformed the dependent variables using an asymptotic transformation to improve normality (Zar 1999). We conducted the analyses using STATA v12.1 Software (StataCorp, 2011). Before running the LMMs, we tested whether our climatic variables were inter-correlated with a Spearman's rho test. The mean correlation between the climatic variables was low (rho $\leq$ 0.37). When running the LMMs in Stata, we used the 'drop collinear variables' option to further control for the possible collinearity between the predicting variables. Moreover, we used the 'i.' prefix in Stata for the snow coverage variable, as this method compared scans with no snow coverage to, respectively, scans with moderate and major snow coverage.

Results

The study groups experienced extreme variance in climatic variables across the data collection periods (Fig. 1). The study animals had 30 days (4.68% of the total observation days) of major snow coverage (i.e. snow covering 50%-100% of the area) and 47 days (7.33%) of moderate snow coverage (i.e. snow covering 1%-49% of the area). Daily rainfall ranged between 0 and 117 millimetres (mean ± SE = 3.96 ± 0.28 millimetres per day). Air temperature ranged between -5.0 and 40.4 ºC (mean ± SE = 15.95 ± 0.13 ºC per day) and relative humidity between 0 and 100% (mean ± SE = 57.53 ± 0.38 % per day).

We obtained a significant model for the LMM run on the proportion of time spent feeding (Wald chi-square (7) = 296.34, $P < 0.001$). Feeding time significantly differed across the months, with a maximum in March and a minimum in July, October and November. Feeding time also differed significantly with the time of day, with peaks in the mid-morning and late afternoon (Table 2; Figs. 2 and 3). The monkeys spent proportionally more time feeding when there was moderate or major snow coverage than when no snow was present (Table 2; Fig. 4). We found no significant effect of daily rainfall on the proportion of time spent feeding (Table 2). High air temperature reduced time spent feeding (Table 2. Finally, we found a positive, though marginally non-significant, effect of relative humidity on the proportion of time spent feeding (Table 2)

We obtained a significant model for the LMM run on the proportion of time spent foraging (Wald chi-square (7) = 64.45, $P < 0.001$). Time spent foraging significantly differed across the months but not in relation to time of day (Table 2; Figs. 2 and 3). The proportion of time spent foraging was significantly greater when there was no snow coverage than when snow coverage was moderate or major (Table 2; Fig. 4). Air temperature was negatively related to the time the monkeys spent foraging (Table 2). Finally, we found no significant relationship between the proportion of time spent foraging and, respectively, daily rainfall and relative humidity (Table 2).

We obtained a significant model for the LMM run on the proportion of time spent moving (Wald chi-square (7) = 29.05, $P < 0.001$). Time spent moving significantly differed across the months but not time of day (Table 2; Figs. 2 and 3). Daily rainfall was negatively related to the time the monkeys spent moving (Table 2) whereas we found no significant effect for snow coverage, air temperature and relative humidity (Table 2; Fig. 4).

We obtained a significant model for the LMM run on the proportion of time spent resting (Wald chi-square (7) = 70.08, $P < 0.001$). The proportion of time spent resting varied significantly across the months, but not across the time of day (Table 2; Figs. 2 and 3). The monkeys spent proportionally more time resting when snow was absent than with moderate snow coverage (Table 2; Fig. 4). We found no difference in resting time between scans with no snow coverage and scans with major snow coverage (Table 2; Fig. 4). Time spent resting was greater when daily rainfall was high than when it was low or absent (Table 2). We found no significant effect of air temperature or relative humidity on the proportion of time spent resting (Table 2).

We obtained a significant model for the LMM run on the proportion of time spent social behaviour (Wald chi-square (7) = 122.35, $P < 0.001$). The proportion of time spent on social behaviour varied significantly across the months but not according to the time of day (Table 2; Figs. 2 and 3). Time spent on social behaviour was not affected by snow coverage or air temperature (Table 2; Fig. 4). The proportion of social time was significantly lower for scans where daily rainfall or relative humidity were higher than for scans where rainfall or humidity were low (Table 2).

Discussion

Our findings show that wild Barbary macaques living in the Middle Atlas Mountains of Morocco face highly variable seasonal climatic conditions which significantly affect their activity budgets. Our results support the marked seasonality of activity budgets in the Barbary macaque for both provisioned groups and for the Moroccan and Algerian wild populations (Fa, 1986; Ménard and Vallet 1997; El Alami et al. 2012). Conversely, activity budgets were largely unaffected by time of day as only feeding time significantly differed across the daylight hours. Seasonal differences in activity budgets across the months have been reported in many primate species and they can be a function of seasonal changes of climatic variables (e.g. Bernstein 1972; Clutton-Brock and Harvey 1977; Hill et al. 2003; Sato 2012). They may also result from seasonal variations in daylight length which constrains how diurnal animals manage their time (e.g. Hill et al. 2003). For example, both provisioned and non-provisioned baboons spend more time feeding in the longer summer days (Hill et al. 2003; van Doorn et al. 2010). In our study population, the monkeys spent more time feeding in winter, due to the presence of snow, and spring (Fig. 2), when food is more abundant than in the dry summer months. Time spent moving or foraging also significantly differed across the months, indicating that the time necessary to search for, and access food was affected by seasonal changes in diet diversity (Ménard 2002). Similarly to other species living in different climatic regions to the Barbary macaque (e.g. *Papio* spp.; Dunbar 1992; Hill 2006; Campos and Fedigan 2009; Sato 2012), resting time peaked during the hot summer months. As such, primates become more sedentary at high temperatures in order to thermo-regulate, regardless of their geographic distribution.

In many diurnal species feeding time is highest in the early morning and late afternoon in response to or in preparation for the night, when opportunities for feeding are low or absent (e.g. Robinson 1984; Chapman and Chapman 1991). Moreover, animals may spend less time feeding during the hottest part of the day, seeking shade to avoid over-heating and to minimise evaporative water loss (e.g. Hill 2006; Campos and Fedigan 2009; Sato 2012). Wild Barbary macaques in the Moroccan Middle Atlas Mountains appear to follow this daily pattern, spending proportionally more time feeding in the mid-morning and late afternoon (Fig. 3). Our results are thus similar to the daily pattern of activity reported in previous studies conducted in the Middle Atlas Mountains (Deag 1985) and the cedar and oak forests of Algeria (Ménard and Vallet 1997).

The monkeys spent proportionally more time feeding and less time foraging when snow coverage was between 1% and 49% of the area than when there was no snow, and more time feeding at lower temperatures. Snow coverage thus appears to be an important factor affecting the feeding ecology of the Barbary macaque. Data could rarely be collected during days of major snow coverage (see Methods) and were thus biased in favour of days of no or moderate snow coverage. As such, our analyses likely under-estimate the role that snow coverage has for the ecology, activity and survival of the macaques.

Our findings support the view that feeding time is reduced when air temperature is high in primate species differing in group size, ecology and geographic distribution (e.g. Dunbar 1992; Campos and Fedigan 2009; Bettridge et al. 2010). The monkeys' response to snow coverage and temperature may represent a strategy to maximize feeding efficiency (Iwamoto and Dunbar 1983; Stephens and Krebs 1986; van Doorn et al. 2010) by attempting to ingest more food at lower temperatures (when the daily energetic requirement for thermoregulation is greater; Hill 2006) and when snow is present. The effect of snow coverage and air temperature on feeding may also be due to the lower quality of food available in the winter months (Ménard 2002). Finally, daily rainfall was negatively associated with time spent moving and in social behaviour, and positively associated with time spent resting. Monkeys appeared to seek shelter and protection during times of heavy rainfall which disrupted their usual ranging patterns and social activity.

Our results highlight the importance to understand to what extent the Barbary macaque is under ecological pressure as a consequence of the extreme climatic variations of the Middle Atlas Mountains. The behavioural flexibility of the Barbary macaque (Ménard 2002) allows this species to cope with the cold winters and hot summer of the Middle Atlas Mountains. However, these extreme climatic conditions can significantly affect the behaviour of the macaques. This is especially true if the current distribution of the Barbary macaque is due to competition for land with humans (Fa 1984; Camperio Ciani et al 2005; Waters et al 2007) rather than due to unconstrained habitat selection. Our results support this view. Several monkeys did not survive the harsh 2008 – 2009 winter. The disappearance of those monkeys was probably due to the fact that the Barbary macaque mainly feeds on the ground; as such, snow coverage significantly reduces access to food sources and forces an increased time feeding. Additionally, feeding terrestrially when snow cover is high means individuals have to sit or stand in the snow and dig through it to access food. This exposes a greater proportion of their bodies, especially extremities, to the cold, reducing body temperature and increasing energy expenditure. To our knowledge, our study is the first to provide evidence of the effect of snow coverage on the behaviour of the Barbary macaque. Our results indicate that particularly cold and snowy winters can dramatically threaten the survival of the Barbary macaque, a species that has significantly decreased in number over the last few years (Lavieren and Wich 2009). A similar, negative effect of snow coverage on survival and feeding ecology has been found in other primate species living in cold climates (Hubei golden snub-nosed monkeys, *Rhinopithecus roxellana hubeiensis*: Li et al. 2009; Japanese macaques, Nakayama et al. 1999). Indeed, the dry summer months and snowy winters of the Middle Atlas Mountains appear to significantly affect the feeding ecology of the Barbary macaque. In the summer when food and water availability are low, macaques are forced to use alternative feeding strategies, such as bark-stripping, to obtain their daily requirements of water and other important nutrients (Ménard and Qarro 1999; Ménard 2002). In our study, snow coverage significantly increased the proportion of time the monkeys spent feeding. The lack of food may also force the monkeys to feed in more open areas where escaping from predators is more difficult (e.g. far away from trees). Moreover, moderate snow coverage significantly reduced the proportion of time the monkeys spent resting. High air temperature constrains this activity and can predict the geographic distribution of primates (Korstjens et al. 2010). Our findings add to Korstjens and colleagues' (2010) study by showing that cold temperatures, rather than increasing temperatures, can also significantly constraint activity budgets, especially for temperate species. Therefore, optimal temperature range may be a better predictor of geographic distribution and ecological stress for a species than maximum or minimum temperature alone.

These considerations, together with the dramatic population decline observed in the last few years (Camperio Ciani et al 2005; van Lavieren and Wich 2009) support the view that the Barbary macaque is under high ecological pressure (Fa 1984; Camperio Ciani et al 2005; Waters et al 2007; van Lavieren and Wich 2009). The cold and snowy winter months and the hot and dry summer months represent two periods of limited availability of food, water and important nutrients (Deag 1985; Ménard 2002; Hanya et al. 2011) that can have negative effects on the survival of macaques. Therefore, despite their behavioural flexibility (Ménard 2002), it appears to be difficult to maintain viable populations of Barbary macaques in the mountainous regions of North-West Africa. In light of this, efforts should be made to create protected areas in the Atlas region at lower altitudes, as the milder climatic conditions might favour population growth (Fa 1984; van Lavieren and Wich 2009).

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TABLE 2 Coefficients and significance of the test variables for the LMMs on the proportion of time the Barbary macaques spent in each of the five activities.

Activity	Variable	Coefficient ± SE	z value	P value
Feeding	Month	-0.03 ± 0.00	-12.00	< 0.001
	Time of day	0.01 ± 0.00	5.85	< 0.001
	Snow coverage			
	No snow vs. 1-49%	0.11 ± 0.03	3.30	< 0.01
	No snow vs. 50%-100%	0.01 ± 0.04	2.81	< 0.01
	Daily rainfall	-0.00 ± 0.00	-0.36	0.72
	Air temperature	-0.01 ± 0.00	-3.44	< 0.01
	Relative humidity	0.00 ± 0.00	1.90	0.06
	Intercept	0.52 ± 0.10	5.23	< 0.001
Foraging	Month	-0.01 ± 0.00	-3.83	< 0.001
	Time of day	-0.00 ± 0.00	-1.71	0.09
	Snow coverage			
	No snow vs. 1-49%	-0.10 ± 0.03	-3.32	< 0.01
	No snow vs. 50%-100%	-0.10 ± 0.04	-2.94	< 0.05
	Daily rainfall	-0.00 ± 0.00	-1.00	0.32
	Air temperature	0.01 ± 0.00	3.84	< 0.001
	Relative humidity	0.00 ± 0.00	0.61	0.54
	Intercept	0.29 ± 0.05	5.54	< 0.001
Moving	Month	0.01 ± 0.00	4.17	< 0.001
	Time of day	-0.00 ± 0.00	-0.35	0.73
	Snow coverage			

	No snow vs. 1-49%	-0.04 ± 0.03	1.34	0.18
	No snow vs. 50%-100%	-0.05 ± 0.03	1.54	0.13
	Daily rainfall	-0.00 ± 0.00	-2.37	< 0.05
	Air temperature	-0.00 ± 0.00	-0.36	0.72
	Relative humidity	0.00 ± 0.00	0.54	0.59
	Intercept	0.16 ± 0.05	3.11	< 0.01
Resting	Month	0.01 ± 0.00	4.48	< 0.001
	Time of day	-0.00 ± 0.00	-1.76	0.08
	Snow coverage			
	No snow vs. 1-49%	-0.10 ± 0.04	-2.81	< 0.01
	No snow vs. 50%-100%	-0.05 ± 0.05	-1.11	0.27
	Daily rainfall	0.00 ± 0.00	3.79	< 0.001
	Air temperature	0.01 ± 0.00	1.31	0.19
	Relative humidity	-0.00 ± 0.00	-1.01	0.31
	Intercept	0.40 ± 0.08	5.15	< 0.001
Social	Month	0.02 ± 0.00	8.82	< 0.001
	Time of day	-0.00 ± 0.00	-1.21	0.23
	Snow coverage			
	No snow vs. 1-49%	-0.01 ± 0.03	0.18	0.86
	No snow vs. 50%-100%	-0.03 ± 0.04	0.67	0.50
	Daily rainfall	-0.00 ± 0.00	-3.69	< 0.001
	Air temperature	-0.01 ± 0.00	-1.62	0.11
	Relative humidity	-0.01 ± 0.00	-3.55	< 0.001
	Intercept	0.38 ± 0.07	5.83	< 0.001

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Figure legends

Fig. 1 Monthly means of daily rainfall (millimetres), air temperature (ºC) and relative humidity (percentage) in the Middle Atlas Mountains, Morocco, across the study period (June 2008 – January 2011). The symbol * indicates months in which there were ≥ 5 days of snow coverage (i.e. days in which snow was covering 1%-100% of the area used by the monkeys)

Fig. 2 Mean monthly percentage of times the Barbary macaques spent on each activity during the year (June 2008 – January 2011). Note that the bars do not always add up to 100% as the Other category was excluded from the analyses (see Methods)

Fig. 3 Mean percentage of time the Barbary macaques spent on each activity in the daylight hours of the day. Note that the bars do not always add up to 100% as the Other category was excluded from the analyses (see Methods)

Fig. 4 Mean percentage ± SE of time the Barbary macaques spent on each activity when snow was absent, covered between 1 and 49% of their home range (i.e. moderate snow coverage), or covered between 50 and 100% of their home range (i.e. major snow coverage)

TABLE 1 Details of the study period (June 2008 – January 2011), composition and number of scan samples collected on the four study groups of Barbary macaques in the Middle Atlas Mountains, Morocco.

Group ID	Study period	Group size	N adult males	N adult females	Total N scan samples collected on each group (mean per day ± SE)	Mean N scan samples collected on each group per month ± SE	Mean N of animals recorded in each scan ± SE (% of study animals recorded per scan)
Flat-face	24 Jun 2008 – 8 Dec 2008	29	11	8	335 (4.0 ± 0.1)	48.6 ± 6.6	9.6 ± 0.1 (50.1%)
	31 Jan 2009 – 9 Sep 2009	11	2	4	250 (2.8 ± 0.1)	43.7 ± 5.7	5.1 ± 0.1 (85.0%)
Large	15 Jan 2009 – 12 Dec2009	39	19	10	146 (3.5 ± 0.2)	30.3 ± 6.5	9.1 ± 0.2 (31.4%)
	13 Jan 2009 – 21 Aug 2009	17	3	3	187 (3.1 ± 0.2)	28.9 ± 5.9	5.3 ± 0.1 (88.3%)
Scarlet	9 Dec 2010 –	27	6	8	489 (5.8 ± 0.2)	69.9 ± 7.8	8.3 ± 0.1 (59.3%)

	28 Jan 2011						
Green	29 Sep 2009 – 28 Jan 2011	18	8	7	1997 (7.2 ± 0.2)	166.4 ± 32.5	9.1 ± 0.1 (60.7%)

Figure 1
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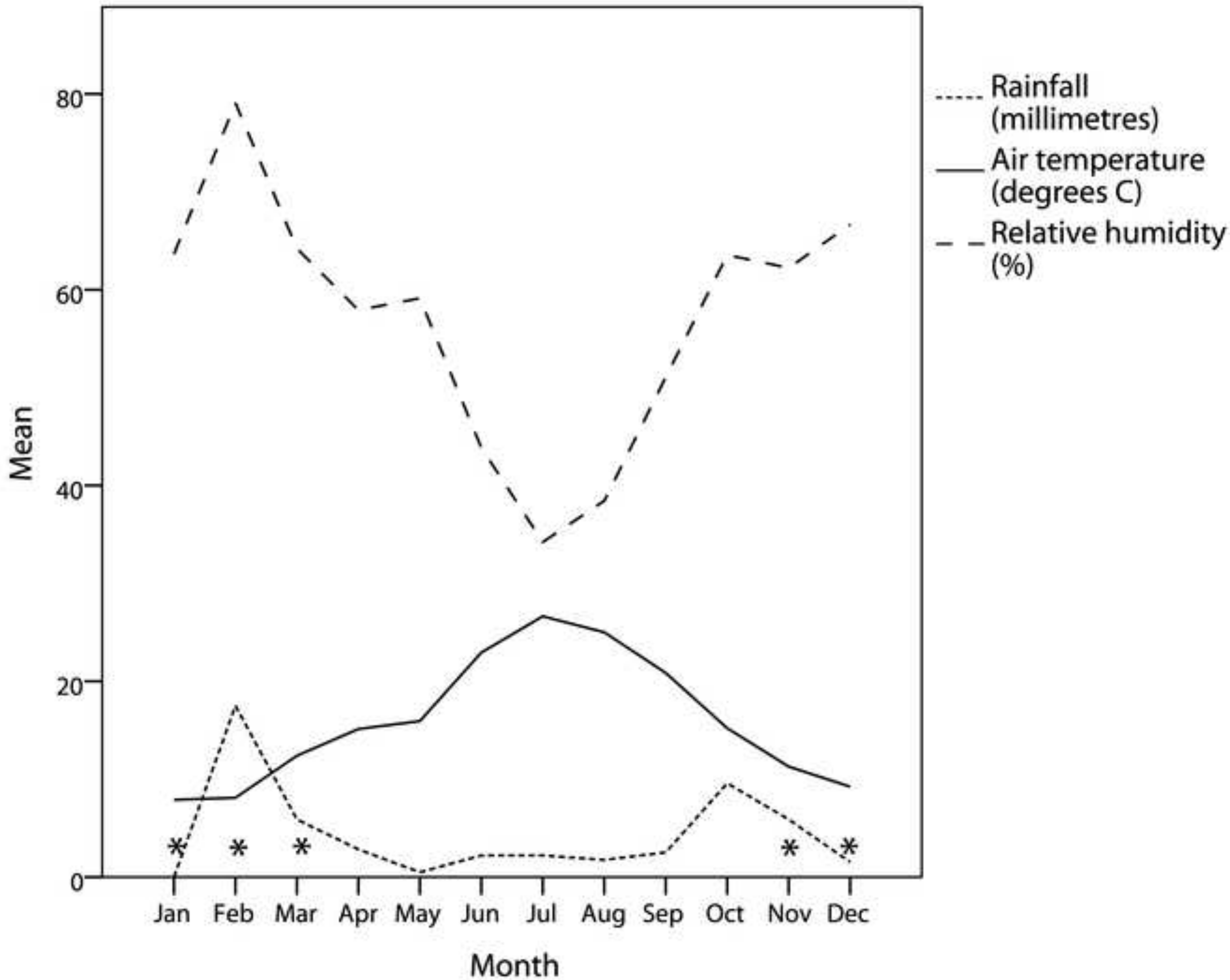

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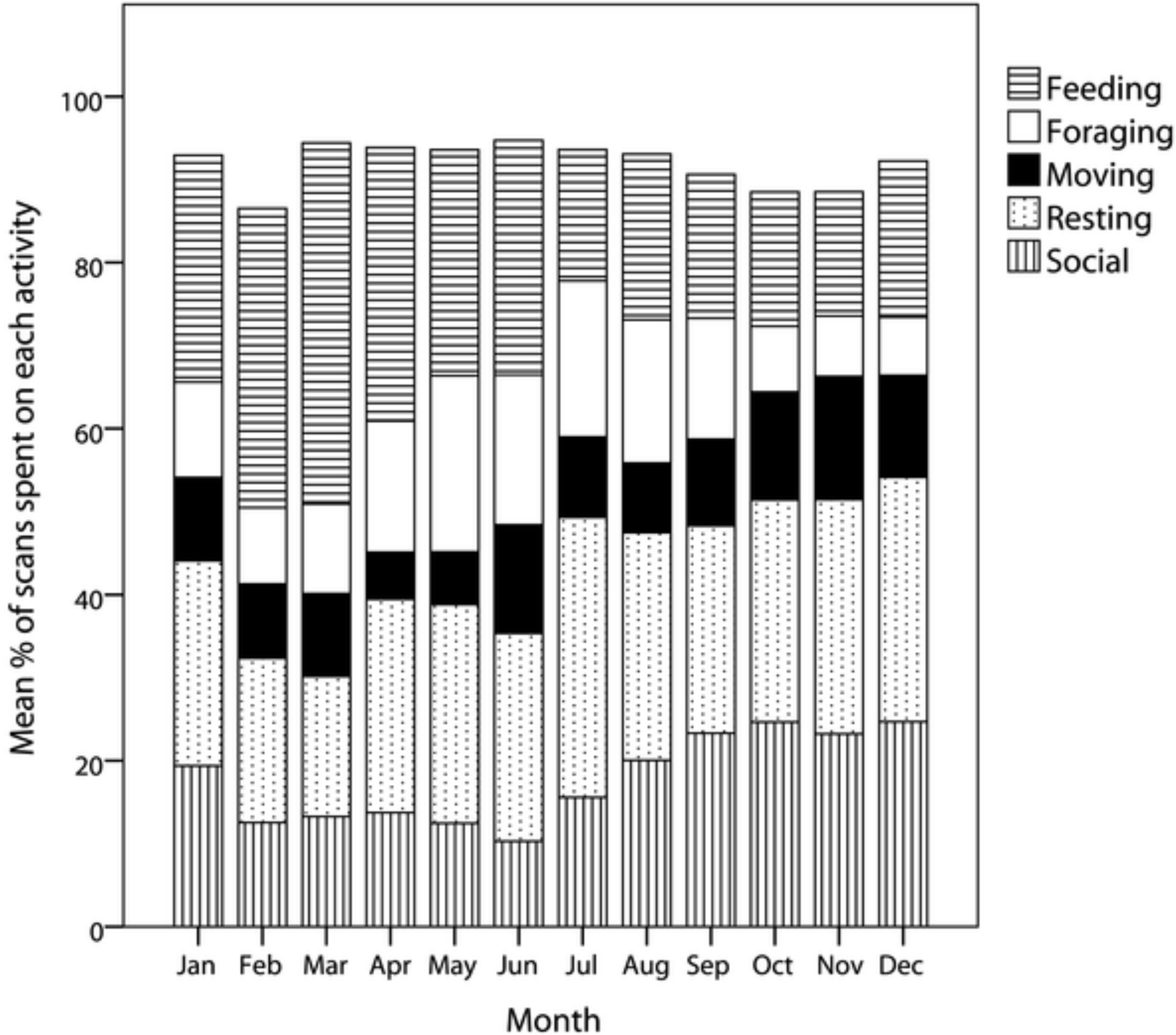

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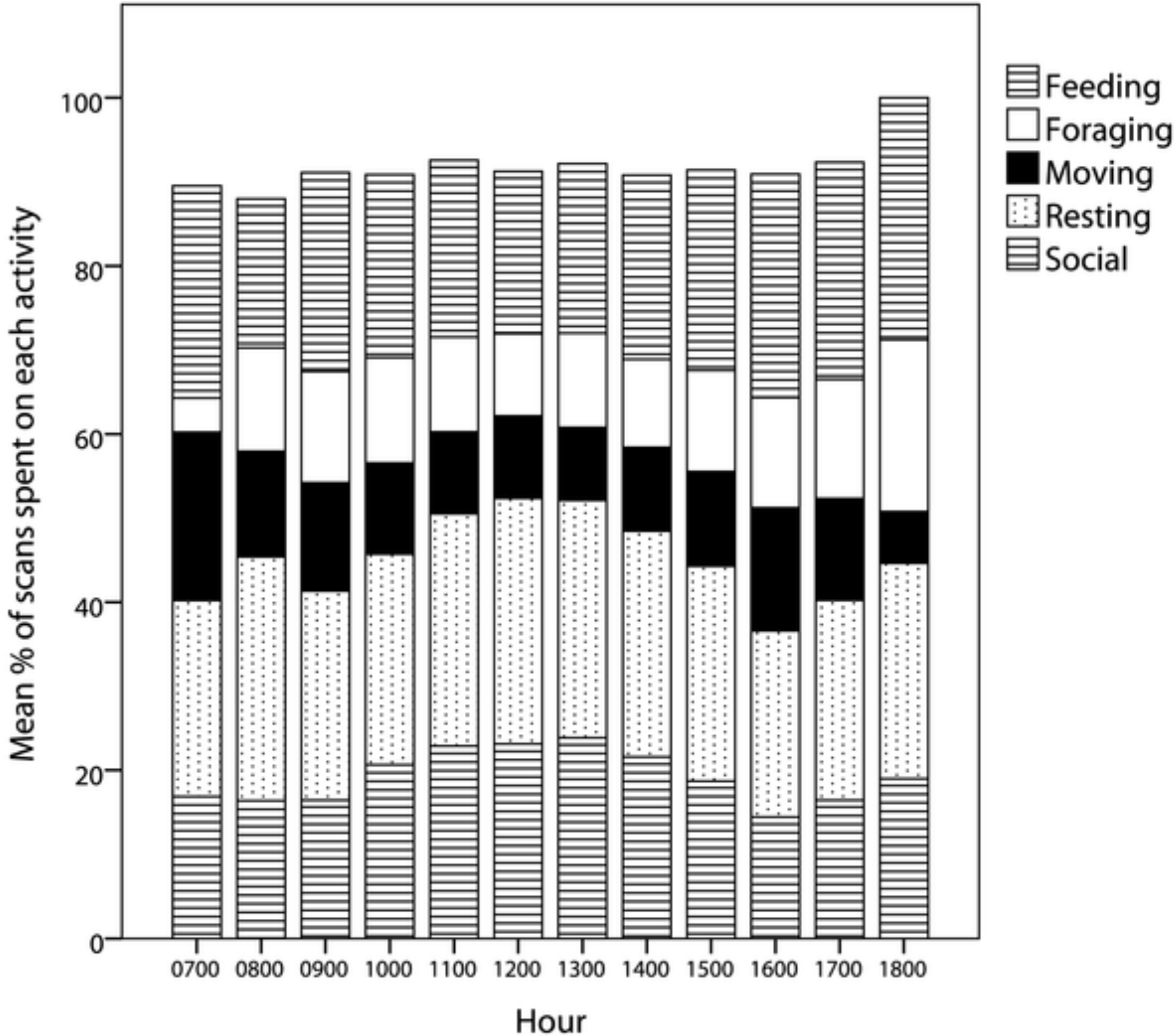

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