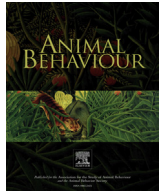




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Thermoenergetic challenges and daytime behavioural patterns of a wild cathemeral mammal

Juan P. Perea-Rodríguez ^{a, b, *}, Margaret K. Corley ^{a, b}, Horacio de la Iglesia ^c,
Eduardo Fernandez-Duque ^{a, d}

^a The Owl Monkey Project, Department of Anthropology, Yale University, New Haven, CT, U.S.A.

^b Yale Reproductive Ecology Lab, Yale University, New Haven, CT, U.S.A.

^c Department of Biology, University of Washington, Seattle, WA, U.S.A.

^d Yale School of Forestry and Environmental Sciences, Yale University, New Haven, CT, U.S.A.

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The circadian thermoenergetics hypothesis (CTEH) suggests that endotherms benefit by being active during the warmer period of a 24 h cycle and by resting when temperatures drop, since this lowers energetic investment in thermoregulation. In accordance with the CTEH, cathemeral (i.e. active during both daytime and night-time) Azara's owl monkeys, *Aotus azarae*, of the Argentinean Chaco increase their daytime activity during the relatively cold winter compared to the summer. Still, it remains unclear whether these behavioural changes are explained by major shifts in energy balance. Thus, we sought to understand how thermal challenges influence the allocation of behaviours during the daytime that tend to conserve energy (resting), increase its availability (foraging) or expend it (travelling). We constructed a priori a set of linear models to evaluate the relationships between daytime behavioural patterns and photoperiod, moonlight, age, reproductive status and hourly, daily and weekly fluctuations in ambient temperatures, as well as some of their interactions. We analysed 4985 20-minute focal samples collected during 0600–2100 hours from 140 recognizable individuals from 15 groups across 13 years. Our results indicate that, from the warmest to the coldest months, daytime resting frequencies decreased by 31%, whereas daytime foraging frequencies increased by 131%, while travelling frequencies remained unchanged. Daytime activity patterns were explained by the interaction between weekly average temperatures and either lunar activity, age class or reproductive status. Generally, daytime activity increased as temperatures decreased seasonally, but this effect was masked during full moons; and infants, juveniles, subadults and solitary adults used the daytime differently. Finally, travelling and foraging increased during longer days or at times of daily maximum temperatures but decreased when these two factors interacted (i.e. long summer days at daily maximum temperatures). In summary, daytime behaviours of *A. azarae* may be structured by thermoenergetic investment, as predicted by the CTEH.

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Mammals have evolved several strategies to thermoregulate efficiently, both by physiological (Angilletta et al., 2010; Clarke & Pörtner, 2010) and behavioural (Terrien et al., 2011) means. In one extreme, exposure to cold temperatures induces investment of metabolic energy in thermogenesis, which is energetically expensive and can be exacerbated by an individual's nutritional state, morphology and reproductive status (Charkoudian & Stachenfeld, 2014). For some taxa, these changes in metabolic energy allocation towards thermoregulation can lead to modifications of their circadian biology, sometimes even resulting in a complete switch in

the distribution of their activity within the 24 h cycle or 'temporal niche'. For example, exposure to cold temperatures may promote increased activity during the warmest period of the 24 h cycle and decreased activity during the coldest period of the 24 h cycle, as this reduces the costs of thermogenesis (Riede et al., 2017; van der Vinne et al., 2014, 2015). On the other extreme, exposure to high ambient temperatures can disrupt general physiological functioning and may result in behavioural and physiological adaptations that increase heat dissipation, or that reduce energy expenditure in order to maximize biochemical efficiency. This can be done by promoting peaks of activity during the relatively cooler periods of the 24 h cycle. Whether challenged by cold or heat, the temporal niche of an individual will depend on the balance

* Corresponding author.

E-mail address: pereajp@gmail.com (J. P. Perea-Rodríguez).

between various factors, including the important costs of thermo-regulation (Hut et al., 2012).

Primates provide a good model to evaluate the ultimate and proximate mechanisms structuring mammalian circadian biology, especially as it relates to our thermoenergetics. The species in this order show many of the activity patterns seen in other mammalian clades, including nocturnality (i.e. activity predominantly throughout the night), cathemerality (i.e. similar activity during the daytime and night-time), crepuscularity (i.e. bimodal patterns of activity with peaks at dawn and dusk) and diurnality (i.e. activity predominantly throughout the day) (Bennie et al., 2014; Santini et al., 2015). Field and captive work on nonhuman primates suggest that their temporal niche is linked to an individual's phylogeny and to ecological and physiological factors that have the potential to modify how individuals invest metabolic energy (Erkert, 2008). That is, the temporal niche an individual occupies depends on the balance between various genetic factors and phenotypic plasticity (Smarr et al., 2013).

Primate activity patterns are generally influenced by nutritional, thermoregulatory and reproductive needs, and by other factors that have direct effects on their survival (e.g. predation). Most of the extant nocturnal primates are prosimians (lorises, tarsiers, lemurs), with diurnality evolving several times in this clade (Bennie et al., 2014). Diurnality is present in all major clades of primates, and studies of some model species suggest that daytime activity patterns are heavily influenced by photoperiod, temperature and food availability (Bray et al., 2017; Erkert, 2008). Crepuscularity is the less prevalent and little is known about its mechanism and the role biotic and/or abiotic factors may play, but the duration of twilight seems to correlate positively with this temporal niche among mammals (Bennie et al., 2014). Finally, building from some preliminary studies in the 1970s and 1980s (Tattersall, 2006) and in the last three decades (Colquhoun, 1998; Donati et al., 2001, 2013), a number of primate taxa have been studied for their cathemeral pattern of activity.

Numerous studies have identified ecological and physiological factors that correlate with the presence of cathemeral activity in primates. For example, high metabolic rates or nutritional deficiencies and high predation risk may promote this behavioural pattern (Curtis & Rasmussen, 2006; Donati et al., 2009; Eppeley et al., 2017). Cold thermal challenges can disrupt important physiological processes (e.g. gonadal and/or immune function) as a result of the energetic demands of thermoregulation (Ellison, 2003; Scholander et al., 1950). On the other extreme, exposure of mammals to high temperatures can interfere with normal physiological functioning (Adolf, 1947). Understanding the environmental factors modulating the temporal niche of cathemeral primates can inform us of the mechanisms regulating the transition from nocturnal to diurnal habits in endotherms (Tattersall, 2008), something our early mammalian ancestors experienced long ago (Gerkema et al., 2013; Maor et al., 2017).

The South American owl monkey (*Aotus* spp.) offers an interesting opportunity to examine the effects different environmental factors can have on temporal niche. Owl monkeys are the only extant nocturnal monkeys in the Americas and the genus, distributed from Panama to Argentina, most likely evolved from a diurnal ancestor (Menezes et al., 2010). Of the 11 species described, only the southernmost species, the 'Mirikina' or Azara's owl monkey, *Aotus azarae*, of northern Argentina and southern Paraguay, has been described as showing cathemeral activity patterns (Fernandez-Duque, 2012; Fernandez-Duque et al., 2010). Compared to species found closer to the equator, *A. azarae* experience the most extreme seasonal changes in daily and yearly ambient temperatures (Erkert et al., 2012; Khimji & Donati, 2014; Mann, 1956). Similar shifts in temporal niche are predicted to happen in

endotherms with wide altitudinal gradients, as temperatures tend to fall as altitude increases. This may be the case, for example, for species such as grey-bellied night monkeys, *Aotus lemurinus*, which are found at altitudes greater than 1500 m above sea level (Defler, 2004), but very little data are currently available on this topic. Therefore, it seems plausible that *A. azarae* experience unique thermoregulatory challenges that other species in the genus do not, making it an adequate model to study how thermoenergetic challenges may influence the temporal niche of an endotherm.

Recent studies have provided strong evidence of the relationship between thermoregulatory challenges and changes in activity patterns. Exposure of food-restricted nocturnal mice to low external temperatures resulted in increased daytime activity, which in turn reduced daily energy expenditure by 6–10% (van der Vinne et al., 2015). These data are the basis for the circadian thermoenergetics hypothesis (CTEH), which proposes that diurnal activity patterns allow endotherms to reduce overall metabolic energy expenditure, especially under energetically challenging situations, such as nutrient deficiency and/or increased predatory risk (Hut et al., 2012; van der Vinne et al., 2014, 2015). Such a strategy may be adaptive if it ultimately provides more resources to invest in other important physiological processes that increase an individual's survival and reproduction (Ellison, 2003). Furthermore, the CTEH highlights the important role a negative energy balance, either due to thermoregulatory energy expenditure, energy expenditure allocated to predatory avoidance and/or hunger, may have had in shaping the evolution of activity patterns in other endotherms (van der Vinne et al., 2014, 2015). The CTEH also provides a framework to examine how nocturnal, crepuscular and cathemeral species experiencing strenuous thermoregulatory challenges during the night-time can benefit by shifting their temporal niche towards the light hours of the 24 h cycle.

In partial support for the CTEH, daily and seasonal activity patterns of wild Azara's owl monkeys are associated with changes in ambient temperature and nutrient availability. *Aotus azarae* display more nocturnal activity during moonlit nights, but the amount of nocturnal activity is secondarily associated with ambient temperature (Erkert et al., 2012; Fernandez-Duque, 2003; Fernandez-Duque et al., 2010). Furthermore, the arrival of the coldest months of the year, when daytime activity is highest (Erkert et al., 2012), coincides with periods when fruit availability is low and individuals switch to ingesting less nutritious but more abundant food items, such as flower buds and leaves (van der Heide et al., 2012). Unfortunately, we do not have detailed information on the ecology of the natural predators of *A. azarae* in our study site, which include jaguarundis, *Puma yagouaroundi*, ocelots, *Leopardus pardalis*, Geoffroy's cats, *Leopardus geoffroyi*, and tayras, *Eira barabara*, but we have witnessed only a few instances of predation attempts by tayras.

What (little) is known about the mechanisms used by owl monkeys to thermoregulate across their geographical distribution, suggests that they are highly sensitive to variations in external temperatures. For example, Scholander et al. (1950) exposed wild three-striped night monkeys, *Aotus trivirgatus*, from Panama to experimental temperatures of 10–30 °C and found that individuals tended to noticeably increase their energy expenditure at values lower than 15 °C. In addition, *A. trivirgatus* from Brazil show similar fluctuations in body temperatures as other nocturnal primates, with the lowest seen between 0700 and 1700 hours and the highest between 1800 and 0500 hours, which is opposite of the pattern observed in a sympatric diurnal monkey (e.g. common marmoset, *Callithrix jacchus*) (Morrison & Simoes, 1962). Furthermore, *A. azarae*, unlike nocturnal owl monkeys that sleep in tree holes, commonly sleep on branches, preferring sleeping trees with light foliage and direct sun exposure during the cold and dry winter and selecting

densely covered sleeping sites during the hot and humid summer (Savagian & Fernandez-Duque, 2017). Similar strategies are used by cathemeral woolly lemurs, *Avahi meridionalis*, to reduce competition and/or reduce predation with other sympatric species (Campera et al., 2017).

Still unclear, however, is whether exposure of *A. azarae* to low ambient temperatures induces major shifts in metabolic energy investment in thermoregulation. Thus, the goal of our study was to investigate how short-term (hourly, daily) and/or long-term (weekly) fluctuations in ambient temperatures may explain the daytime activity patterns of wild Azara's owl monkeys, who are naturally active both during the daytime and the night-time. Specifically, we wanted to understand how daily and weekly changes in temperature may structure the allocation of time during the light portion of the 24 h cycle to behaviours directly or indirectly related to energy conservation (resting), energy intake (foraging) and energy expenditure (travelling). We hypothesized that individuals would benefit from increasing the duration of daytime activity on days with relatively lower temperatures because this would reduce their overall metabolic energy expenditure allocated for thermoregulation. Under this hypothetical scenario, we predicted that individuals generally would be energetically deficient at colder temperatures and would show lower frequencies of daytime resting and travelling (energetically costly, compared to foraging) and higher daytime foraging frequencies (energetically beneficial, compared to resting or travelling). We further predicted that during the coldest days monkeys would be more active for the duration of the warmest period of the day and would display higher frequencies of active behaviours at the times of daily maximum temperatures, especially behaviours that increase energy balance, as this presumably further reduces thermoregulatory investment.

METHODS

Study Site and Animals

The study site is located in South America in the Formosa province of northern Argentina, 150 km south of the Paraguayan border (58°11'W, 25°58'S). The area, which contains a mixture of grasslands, savannahs and dry and wet gallery forests, is characterized by marked seasonal changes in photoperiod, rainfall, temperature and food productivity (Fernandez-Duque, 2003; Fernandez-Duque & van der Heide, 2013; van der Heide et al., 2012). Behavioural and demographic data were collected from individuals in a population of Azara's owl monkeys that has been studied as part of the Owl Monkey Project, a 23-year project focused on the study of the evolution, genetics, ecology, behaviour and reproductive physiology of owl monkeys (Fernandez-Duque et al., 2016, 2020). In this area, these medium-sized (~1.2 kg) primates are commonly found in semideciduous forests along the banks of rivers and in naturally isolated patches of forests surrounded by grasslands.

Owl monkeys in this population are pair-living and sexually and genetically monogamous, and both parents care for their young (i.e. biparental care) (Fernandez-Duque et al., 2020; Huck et al., 2014, 2019). They are seasonal breeders and commonly produce a single infant once a year usually born between late September and December (Fernandez-Duque et al., 2002; Huck et al., 2011). Individuals live in small (i.e. 2–6 individuals) social groups that include a reproductive pair and some young (Fernandez-Duque, 2016). Males and females disperse from their natal group when they are 2.2–4.9 years of age (Fernandez-Duque, 2009). After dispersal, adults range solitarily until they enter an existing group, something that may take several years or may never happen at all, by expelling a same-sex reproductive resident, at which point the

two adults begin the pair-bonding process (Fernandez-Duque & Huck, 2013). These solitaires may face different challenges by being alone, compared to pair-bonded adults, including thermoregulatory challenges when experiencing cold weather, as they cannot huddle with other group members (Terrien et al., 2010), or they may be at a disadvantage trying to avoid predators or competing for resources.

Data Collection

Behavioural, demographic and climatological data were extracted from the Owl Monkey Project's relational database. Climatological data was used to determine fluctuations in photoperiod, ambient temperature and moonlight. The behavioural data was used to describe short- and long-term changes in resting, travelling and foraging behaviours. The individual's age class was used to explore whether thermoregulatory demands may differ between nutritionally dependent infants (≤ 6 months), nutritionally independent juveniles and subadults (6.1–48 months) and adults (48+ months) (Huck et al., 2011). Similarly, the focal animal's reproductive status (i.e. solitary adult or member of a group) was used to examine whether monkeys respond differently to climatological changes while solitaires or pair-bonded.

Behavioural and Demographic Data

We collected these data following ethograms and sampling methods from the Monogamous Primates Project, which have been standardized to study several species of pair-living New World monkeys (Fernandez-Duque et al., 2013, 2020). Each focal sample commenced once the animal was encountered and identified by the observer, and the initiation time was recorded. Behavioural states (i.e. resting, travelling, foraging) were recorded every 2 min for 20 min. Animals were considered to be resting when they were asleep or standing still, or travelling when they moved from one location to another (not while foraging). Foraging was considered when the focal animal searched for, manipulated or ingested food items. Other behavioural states (e.g. social behaviours) were recorded during the sampling but excluded for the current analyses since these behaviours can be affected by other environmental factors.

For each 20 min focal observation we calculated the frequencies for the behavioural states of interest. That is, we divided the total number of intervals in which each animal was in the behavioural state of interest by the number of intervals in each focal when the animal was visible (usually 10). On 142 occasions we did not complete the focal sample because the focal animal was lost (fewer than 10 total 2 min intervals). For these cases the frequencies were calculated out of the available 2 min intervals in the 20 min focal sample when we actually observed the animal. Often, we did focal sampling from multiple members of the same group during the same sampling period. In the majority of cases we waited 10 min before starting consecutive focal samples on the same individual but there were 32 instances when an animal was observed for three consecutive focal samples.

We searched for 20 min focal samples collected during 0600–2100 hours between January and December for 13 years between 2001 and 2015 (Supplementary Table S1). This resulted in 4985 focal samples out of the 6377 available in the database. We used data from 140 subjects living in 15 different groups found in, or around, defined territories. We collected all of the data from habituated individuals that could be discriminated from one another by radiocollars or bead collars, body size and/or natural distinguishing markings.

Climatological Data

We downloaded daylength and lunar fraction data from the U.S. Navy online data services (<http://aa.usno.navy.mil/data/index.php>). We measured hourly ambient temperature with Stowaway XTI and HOBO data loggers, set up in the camp at the entrance to the study area. We used hourly temperature measurements to calculate the parameters of interest for ambient temperature (see below). There were 11 instances (1 in 2013 and 10 in 2014) when the temperature data loggers recorded abnormally high values (e.g. 56 °C on 14 November 2014 at 1800 hours), given the highest historical values recorded by the Owl Monkey Project (45 °C; E. Fernandez-Duque, personal observation). We assumed that these recordings were incorrect due to some malfunction of the loggers and assigned the maximum recorded temperature on the site to these instances.

Data Preparation and Exploratory Analyses

We searched the Owl Monkey Project's database to extract focal samples collected between 0600 and 2100 hours, and matched them to the demographic, behavioural and climatological factors of interest using the 'dplyr' package (Wickham & Francois, 2015; R Core Development Team, 2000). We visualized data using the 'ggplot2' package (Wickham, 2010).

Analyses and Model Parameter Selection

We took an information-theoretic approach (Burnham & Anderson, 2002) to build and compare linear mixed models ('lme4' package: Bates et al., 2014; 'glmmTMB' package: Brooks et al., 2017) that could explain the strength of relationships between short- (hourly, daily) and long-term (weekly) changes in ambient temperature, photoperiod, available moonlight, age, reproductive status and patterns of daytime behaviour. For model building, we selected parameters that we considered to be biologically relevant to the chronobiology and energetics of owl monkeys, based on some of our previous findings (Erkert et al., 2012; Fernandez-Duque, 2003; Fernandez-Duque et al., 2010), our understanding of mammalian physiology and behaviour and our experience working with the study species and other owl monkey species in captivity and in the wild. Data from captive and wild owl monkeys indicate important relationships between short- and long-term variations in ambient temperature and the structuring of their daily activity patterns (Fernandez-Duque, 2012).

To incorporate this prior knowledge, we used hourly (the time when the focal sample commenced) temperatures, as well as daily and weekly mean, minimum, maximum and temperature ranges, all calculated from the hourly measures recorded on site. We also considered the daily number of hours that temperatures dropped below 5 °C and 10 °C on the day the focal sample was collected, as well as for the week prior since it has been suggested that temperatures around that range may induce energy allocation towards thermoregulation (Fernandez-Duque et al., 2010; Savagian & Fernandez-Duque, 2017; Scholander et al., 1950).

We considered the fraction of illuminated moon as an indicator of available moonlight on the night before each focal sample was collected, as well as daylength as a measure of photoperiod, given the strong evidence in favour of a relationship between these abiotic factors and activity in *A. azarae* (Erkert et al., 2012; Fernandez-Duque, 2006). We added models with the subject's age class (i.e. dependent infant, independent juvenile or subadult, solitary adult, pair-bonded adult; Huck et al., 2011), social status (i.e. member of a group or solitary; Huck & Fernandez-Duque, 2017) and an index for how close the temperature was to the daily

maximum temperature at the time the focal observation was taken (i.e. ratio of the temperature when monkeys were sampled and the daily maximum temperature). Male and female owl monkeys are behaviourally and morphologically remarkably similar, except in their reproductive physiology and behaviour. Importantly, pair-bonded adults have similar activity budgets as they are constantly together and they forage, travel and sleep together (Fernandez-Duque, 2011); thus, we did not include the subject's sex in our model set.

In addition, we included models with the interaction between each of the daily and weekly temperature measures and either the fractal moon, age class or reproductive status. Finally, we included models for the separate interactions between daylength and each of the daily and weekly measures of temperature, or with either age class, reproductive status or fractal moon. Using the parameters described above, we constructed an a priori set of 77 linear models that quantified the relationships between measures of daily and weekly ambient temperature on frequencies of daytime resting, travelling and foraging during a 20 min focal sample (Supplementary Table S2). We checked for autocorrelation in our outcome variables using correlograms. None of the models in our set included more than one variable calculated from our hourly measures, as this reduces multicollinearity and was beyond the scope of our study.

We first completed the model selection process for frequencies of resting, travelling and foraging using the complete data set of 4985 focal samples that performed well in explaining each of the three behavioural outcomes. Second, to determine how frequencies of travelling and foraging were distributed throughout the day, we completed the model selection process using the hour of day when focal samples were taken (i.e. hours after midnight) as the outcome variable, on a subset of observations that excluded all focal samples that had resting behaviour frequencies less than or equal to 0.30 ($N = 3464$, 138 individuals from 14 groups, 13 years during 2001–2015). That is, for these focal samples, the focal animal was recorded as active during 70% (7 of 10) of the 2 min focal samples. The second analysis allowed us to estimate which model(s) performed well in explaining the distribution of the times, during the daytime, when animals were travelling and foraging.

Model Selection Criteria

We used GLMMs to fit frequencies for resting, travelling and foraging per 20 min focal sample, and we used LMMs to fit data for the time (i.e. hour during the daytime) when active behaviours were performed. We determined which approach (GLMM versus LMM), including the specified family distribution and link function, to use after fitting different distributions to the residuals of each of our four outcome variables and comparing Akaike information criterion (AIC) values between each fit. This was done using the 'fitdistrplus' package (Delignette-Muller & Dutang, 2015). GLMMs included a beta, zero-inflated distribution and LMMs were fitted using a Gaussian distribution.

We calculated the corrected Akaike information criterion (AICc) for each model within each of the model sets for each outcome variable and utilized the differences between the AICc of the best-fit model and each additional model in the set ($\Delta AICc$), cumulative Akaike weights (AICc weights), log likelihoods and evidence ratios to assess the fit of each candidate model to our outcome variables (Anderson et al., 2001; Burnham & Anderson, 2002; Symonds & Moussalli, 2011). It is highly recommended that the possible consideration of a best-fit model from a given set be decided after careful consideration of several indicators; namely, evidence ratios, AICc and $\Delta AICc$ equalling zero, and AICc weights (Burnham &

Anderson, 2002). We considered only one model if it had an AICc larger than 0.90 (Burnham & Anderson, 2002).

When no single model reached the criteria to be considered 'best' for purposes of inference and interpretation (i.e. AICc weight > 0.90), we calculated model-averaged parameter estimates for the parameters in models with cumulative AICc weights up to 0.95 (i.e. 95% confidence set of best-ranked models: Symonds & Moussalli, 2011), as this provides a relatively more stabilized strategy for making inferences under circumstances where there are multiple best-fit models (Burnham & Anderson, 2002). For the parameters in the 95% confidence model set, we first added the AICc weights of all of the models in the complete set in which the parameter of interest was present and then calculated their model-averaged estimates and standard errors. The sum of the AICc weights is used to assess the probability that a single parameter would be present in the best-fit model(s) if a new data set was similarly analysed (Burnham & Anderson, 2002). We used the 'AICcmodavg' package to calculate AICc and the other model indices mentioned above, as well as model-averaged parameter estimates (Mazerolle, 2013).

Ethical Note

All of the procedures used in this study conformed to Argentinean laws and were approved by the National Wildlife Directorate in Argentina, as well as by the animal research committees of the Zoological Society of San Diego, University of Pennsylvania and Yale University. In addition, the animal procedures in the study followed the guidelines for the treatment of animals for research recommended by the ASAB/ABS.

RESULTS

Ambient Temperature and Daytime Behavioural Patterns

Hourly temperatures oscillated throughout the day and were generally lowest before sunrise and highest at mid-afternoon (Fig. 1). Similarly, monthly ambient temperatures fluctuated throughout the year in a clear seasonal pattern (Table 1). The warmest monthly average temperatures were recorded in January (mean $\pm$ SE = 27.6 ± 0.1 °C) and the coldest in July (16.5 ± 0.1 °C).

Frequencies for all three behaviours varied throughout the day. Generally, average daytime resting frequencies were higher early in the morning, peaking at midday, and decreased towards the end of the day. During the summer months, daytime travelling frequencies were generally highest early in the morning and decreased throughout the day, whereas they remained high at midday during the winter months. Frequency of daytime foraging was highest between 1000 and 1600 hours and lowest before 0600 and after 2000 hours.

Daytime behavioural patterns varied throughout the year. The highest average frequencies of daytime resting were recorded during January (warmest month) and the lowest ones in February and July. Average daytime travelling frequencies were lowest in January and between July and September and highest during May. Daytime foraging frequencies were highest in April and July and lowest in January (Table 1).

Comparing behaviour frequencies between the warmest (January) and coldest (July) months, the monkeys decreased about 31% their mean daytime resting (mean $\pm$ SE: 0.35 ± 0.02 versus

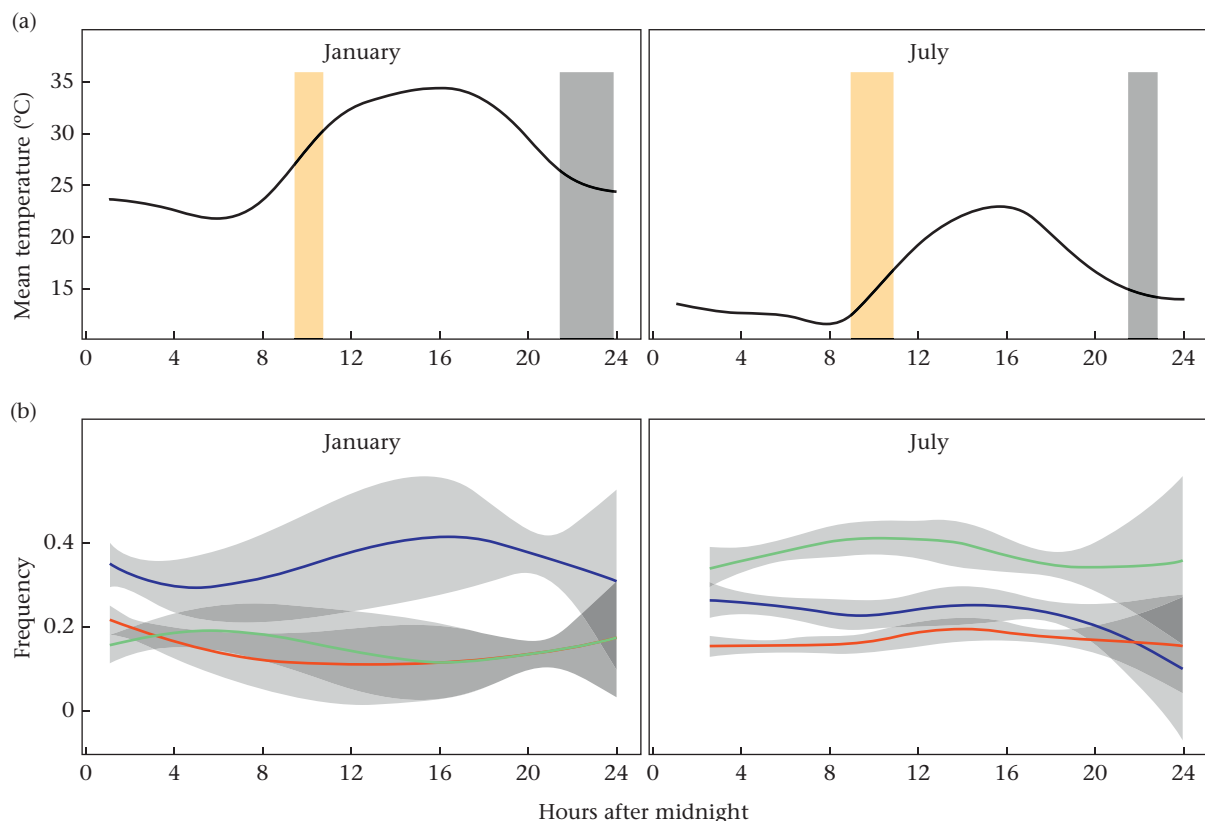


Figure 1. Daily variation in ambient temperature and behavioural patterns on the typically warmest and coldest months of the year averaged over the 13 years sampled. (a) Representative figures displaying daily fluctuations in mean temperature and in sunrise (yellow bars) and sunset (grey bars) times in January and July. (b) Daily mean frequency of resting (blue), travelling (red) and foraging (green) behaviours per 20 min focal observation during the warmest month (January; $N = 312$ focal samples, 60 individuals from 13 groups) and the coldest month (July; $N = 897$ focal samples, 95 individuals from 15 groups), averaged over the 13 years studied. The lines represent the mean and the grey areas describe the 95% confidence interval.

Table 1
Summary of monthly average temperatures and frequencies of resting, travelling and foraging per focal sample throughout the year, all 13 years sampled

Month	Mean ambient temperature (°C)	Freq. of resting	Freq. of travelling	Freq. of foraging
January Warmest (N = 312)	27.6 ± 0.1	0.35 ± 0.02	0.17 ± 0.01	0.16 ± 0.01
February (N = 459)	26.6 ± 0.1	0.24 ± 0.01	0.18 ± 0.01	0.24 ± 0.01
March (N = 230)	25.0 ± 0.1	0.30 ± 0.02	0.21 ± 0.01	0.30 ± 0.02
April (N = 153)	21.1 ± 0.2	0.27 ± 0.02	0.21 ± 0.01	0.38 ± 0.02
May (N = 376)	19.3 ± 0.2	0.25 ± 0.01	0.26 ± 0.01	0.30 ± 0.01
June (N = 440)	17.5 ± 0.5	0.26 ± 0.01	0.18 ± 0.01	0.29 ± 0.01
July Coldest (N = 897)	16.5 ± 0.1	0.24 ± 0.01	0.17 ± 0.01	0.37 ± 0.01
August (N = 791)	18.8 ± 0.2	0.25 ± 0.01	0.17 ± 0.01	0.33 ± 0.01
September (N = 401)	20.1 ± 0.2	0.27 ± 0.01	0.17 ± 0.01	0.26 ± 0.01
October (N = 392)	24.2 ± 0.2	0.29 ± 0.01	0.23 ± 0.01	0.20 ± 0.01
November (N = 312)	25.3 ± 0.1	0.28 ± 0.01	0.22 ± 0.01	0.20 ± 0.01
December (N = 222)	27.1 ± 0.1	0.30 ± 0.02	0.22 ± 0.01	0.19 ± 0.01

The averages include 4985 focal samples (N = 140 individuals from 15 groups). Data are presented as averages and standard errors.

0.24 ± 0.01), while daytime travelling remained unchanged (0.17 ± 0.01 versus 0.17 ± 0.01). In contrast, daytime foraging frequencies showed a 131% increase between the warmest and coldest months (0.16 ± 0.01 to 0.37 ± 0.01) (Fig. 1, Table 1).

Best-fit Models for Patterns of Resting, Travelling and Foraging

Eight of the 77 models in the a priori set best explained the variation in the frequencies of daytime resting (Supplementary Table S3). The parameters in these models were as follows: weekly mean temperature*reproductive status (M42); daily mean temperature*reproductive status (M24); weekly mean temperature*available moonlight the night before sampling (M40); weekly mean temperatures (M8); weekly mean temperature*age class (M41); daily maximum temperature*reproductive status (M30); daylength*weekly mean temperature (M70); temperature at the time when focal samples were collected*reproductive status (M21). Evidence ratios indicated that M42 had 102 times more explanatory power than M21.

Travelling frequencies were also best explained by several models in the set (Supplementary Table S3). The parameters in these 12 models were as follows: daily maximum temperature*age class (M29); weekly mean temperature*age class (M41); daily maximum temperature*reproductive status (M30); daily maximum temperature*available moonlight the day prior to sampling (M28); weekly mean temperature*available moonlight the night prior to focal sampling (M40); daily maximum temperatures (M4); weekly mean temperature*reproductive status (M42); weekly maximum temperature*age class (M47); weekly maximum temperature*reproductive status (M48); weekly mean temperatures (M8); weekly maximum mean temperature*available moonlight the night prior (M46); and weekly maximum temperatures (M10). Evidence ratios indicated that M26 had 123 times more explanatory power than M10.

Daytime foraging frequencies were best explained by five models in the set (Supplementary Table S3), with the interactions between the following variables: weekly mean temperature*age class (M41); daylength*weekly mean temperature (M70); weekly mean temperature*available moonlight the night prior to focal sampling (M40); weekly mean temperatures (M8); and weekly mean temperature*reproductive status (M42). Evidence ratios indicate that M41 had 32 times more explanatory power than M42.

Since several models were selected as the best-fit models for resting, travelling and foraging frequencies, model-averaged parameter estimates were based on the best-fit models with cumulative AICc weight of up to 0.95 (i.e. 95% confidence set of best-ranked models: Symonds & Moussalli, 2011). Resting patterns were

explained best by five different parameters contained in the first four best models (Table 2). The sum of the AICc weights of the models that included weekly mean temperature as a parameter was 0.82, indicating that this parameter would be predicted to appear in the best-fit model explaining daytime resting patterns 82% of the time, if a different set of focal samples were analysed (Burnham & Anderson, 2002). The sum of the weights for all the models where reproductive status and daily maximum temperatures appeared in the model were 0.76 and 0.12, respectively. Finally, the available moon fraction the night before focal samples were taken had a sum of AICc weights equalling 0.09, whereas the sum of for the individual's age class was 0.04.

Model-averaged parameter estimates for daytime resting frequencies had a positive relationship with weekly mean temperature (mean ± SE = 0.02 ± 0.00), whereas a negative relationship was found with reproductive status (solitaries: -0.05 ± 0.07), suggesting that daytime resting increased as weeks became warmer and that pair-bonded and solitary adults used the daytime differently (Fig. 2). Additionally, estimates for daytime resting frequencies showed a positive relationship with daily maximum temperatures and available moonlight, indicating that individuals tended to rest more as days became increasingly warmer and as the moon became full (0.12 ± 0.01 and 0.09 ± 0.05, respectively). Finally, model-averaged estimates for an individual's age class indicated that daytime resting frequencies were lower in younger individuals (infants: -0.01 ± 0.12; juveniles: -0.15 ± 0.07).

Daytime travelling patterns were explained by five parameters from the 95% confidence set of best-ranked models. The sums of AICc weights showed that age class would be included in the best-fit model 73% the time (0.73), whereas daily maximum temperature was expected to be in the best explanatory factors models 60% (0.60) of the time. Reproductive status, moon fraction and weekly mean temperatures had sums of AICc weights of 0.10, 0.10 and 0.05, respectively. Model-averaged estimates for travelling frequencies were positively related to an individual's age class, with infants and juveniles having higher frequencies than adults (infants: 0.35 ± 0.01; juveniles: 0.06 ± 0.06). Daytime travelling frequencies were lower as the moon fraction increased, and estimates for reproductive status revealed that solitaries generally travelled less (-0.01 ± 0.06). This indicates that daytime travelling was less frequent during full moon and that solitary adult monkeys travelled less overall during daytime. Estimates for weekly average temperatures showed a positive relationship with daytime travelling frequencies, suggesting owl monkeys travel more as temperatures begin and continue to rise (0.02 ± 0.00).

Daytime foraging was best explained by four parameters found in three models. The sum of AICc weights for each parameter

Table 2

Model-averaged estimates for parameters for each behavioural outcome variable, based on models with cumulative AICc weights of up to 0.95 (i.e. 95% confidence set of best-ranked models)

Outcome variable	Parameter	Σ AICc weight	Model-averaged estimate	SE	95% CI
Resting frequencies	Weekly mean temperature	0.82	0.02	0.00	0.02, 0.03
	Reproductive status – solitary	0.76	–0.05	0.07	–0.19, 0.08
	Daily maximum temperature	0.12	0.02	0.01	0, 0.04
	Moon fraction	0.09	0.12	0.05	0.02, 0.22
	Age class				
	Infant/juvenile/subadult	0.04			
Travelling frequencies	Infant		–0.01	0.12	–0.29, –0.02
	Juvenile/subadult		–0.15	0.07	–0.01, 0.03
	Age class				
	Infant/juvenile/subadult	0.73			
	Infant		0.35	0.01	0.15, 0.55
	Juvenile/subadult		0.06	0.06	–0.05, 0.18
Foraging frequencies	Daily maximum temperature	0.60	0.02	0.00	0.01, 0.02
	Reproductive status – solitary	0.10	–0.01	0.06	–0.21, 0.01
	Moon fraction	0.10	–0.04	0.05	–0.13, 0.05
	Weekly mean temperature	0.05	0.02	0.00	0.02, 0.03
	Weekly mean temperature	0.91	–0.04	0.00	–0.05, –0.03
	Age class				
	Infant/juvenile/subadult	0.49			
	Infant		–0.31	0.11	–0.53, –0.08
	Juvenile/subadult		0.21	0.07	0.08, 0.34
	Photoperiod	0.32	0.12	0.02	0.09, 0.16
	Moon fraction	0.10	0.01	0.05	0.00, 0.2

Presented are the parameter names, as well as the sum of the Akaike weights of all the models in the set with the parameter of interest present, the parameter estimate and standard error, and the 95% confidence interval for the estimate.

indicated that weekly mean average temperatures would be present in the best-fit model in similar analyses 91% of the time, whereas age class, photoperiod and available moonlight (on the night prior) would be selected 49%, 32% and 10% of the time,

respectively (Table 2). The model estimates for daytime foraging frequencies and weekly average temperatures was negative (-0.04 ± 0.00), suggesting that individuals decreased their time spent foraging as weekly ambient temperatures began to increase

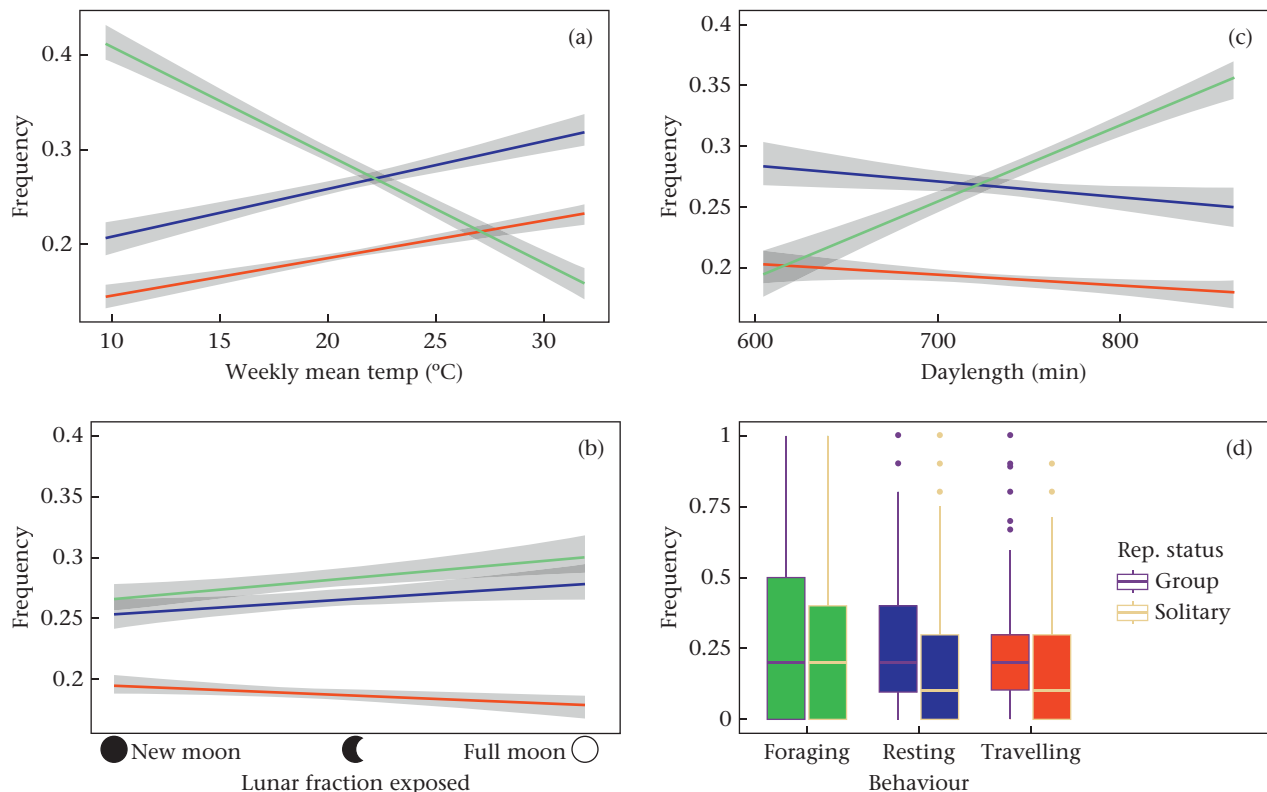


Figure 2. Changes in daytime resting (blue), travelling (red) and foraging (green) behaviours on any given day throughout the year per 20 min focal sample in relationship to (a) weekly mean temperature, (b) available moonlight, (c) photoperiod and (d) reproductive status ($N = 4985$ focal observations, 140 individuals, 15 groups from 13 years collected during 2001–2015). In (a–c), the lines represent the cumulative mean and the shaded areas describe the 95% confidence interval. In (d), the box plots represent the median, first and third quartiles and outliers.

throughout the year (Fig. 2, Table 2). In addition, estimates showed that daytime foraging became more frequent as infants (-0.31 ± 0.11) continued to develop into juveniles/subadults (0.21 ± 0.07), as days became longer (0.12 ± 0.01) and as the available moonlight increased (0.10 ± 0.05) (Fig. 2).

Best-fit Models for the Timing of Daytime Active Behaviours

The distribution of the time during the daytime when active behaviours were recorded (i.e. focal samples with resting behaviour frequencies ≤ 0.30 ; $N = 3464$ focal observations, 138 individuals, 15 groups, collected over 13 years) was best explained by a single model in our set with the interaction between daylength and an index of how close the temperature was at the time focal samples were collected to the daily maximum temperatures as a parameter (M77: AICc weight = 1.00; Fig. 3).

The estimates for the best-fit model indicated that daytime travelling and foraging behaviours became most frequent as days became longer (2.30 ± 0.26) or when temperatures reached the maximum daily temperature (53.13 ± 12.28), but became less frequent when these two factors interacted (-2.91 ± 0.34). That is, travelling and foraging behaviours became less common when days were long (midsummer) at the time when maximum temperatures arrived.

DISCUSSION

We sought to examine the circadian thermoenergetics hypothesis (CTEH), which suggests that mammals and other endotherms reduce metabolic energy expenditure by being active during the warmest period during the 24 h cycle (Hut et al., 2012; van der Vinne, 2014, 2015). To do so, we analysed the relationship between ambient temperature and the daytime activity patterns of wild, cathemeral Azara's owl monkeys from Formosa, Argentina. More specifically, we studied the relationship between daily and weekly changes in ambient temperature and photoperiod, available moonlight, age and reproductive status with the daytime frequencies of behaviours that tend to reduce (resting), utilize (travelling) and replenish/increase (foraging) metabolic energy. In addition, we explored how ambient temperatures and the other factors mentioned may explain the distribution of travelling and foraging throughout the daytime. We predicted that monkeys

would be energetically deficient during the relatively cold winter months and as a result would rest and travel less and forage more at lower temperatures because this behavioural shift restores energy balance. Furthermore, we predicted that, independent of season, individuals would further benefit by scheduling active behaviours when daily maximum temperatures occurred, as this presumably further decreases thermoregulatory costs.

Our findings provide observational evidence that a wild, relatively small primate undergoes seasonal changes in its daytime behavioural patterns due to fluctuations in energy allocation that result from an increased investment of metabolic energy in thermoregulation. This was evident by the increased frequencies of daytime behaviours that tended to increase energy intake (i.e. foraging) and by the decrease in the frequency of behaviours that generally conserved (i.e. resting) metabolic energy during colder temperatures. More specifically, during the coldest months, compared to the warmest months, individuals decreased the frequency of daytime resting by 31% but increased daytime foraging frequencies increased by 131% (travelling frequencies remained unchanged). Frequencies of resting and travelling behaviours were best explained by models with parameters representing daily and weekly variations in ambient temperature, suggesting that resting patterns are mediated by short- and long-term costs of thermoregulation. Furthermore, this can be exacerbated by the available moonlight, that is, daytime resting increases as more of the moon becomes exposed, whereas the opposite is seen for daytime travelling. In addition, other parameters, such as age class and reproductive status were included in the best explanatory models suggesting that activity patterns may also be mediated by developmental/life-history factors. Frequencies of foraging behaviours were best explained by long-term (weekly) measures of ambient temperatures, the available moonlight the night before sampling, photoperiod and the individual's assigned age class. Model-averaged parameter estimates revealed that daytime foraging increased as weeks became colder throughout the year, but decreased as more of the moon became exposed. Finally, focal samples with the highest frequencies of travelling and foraging (i.e. focal samples with resting frequencies ≤ 0.30) became more common during the daytime as temperatures reached the daily maximum temperatures and as the daylength increased, but became rare when these two factors interacted, that is, during the longest day when maximum daily temperatures arrived.

Our results support previous studies on this population of owl monkeys showing that daytime activity is strongly related to changes in ambient temperature (Erkert et al., 2012; Fernandez-Duque, 2003; Fernandez-Duque et al., 2010; Fernandez-Duque & Erkert, 2006). Specifically, it was previously found that the highest levels of daytime activity, and the lowest levels of night-time inactivity, are seen during the coldest months. Similarly, our results show that when experiencing the thermal challenges of the winter, monkeys decreased the frequency of daytime energetically conservative (i.e. resting) behaviours and energetically costly (i.e. travelling) behaviours, and spent most of (warmest period during) the day performing behaviours that replenished energy reserves (i.e. foraging). Although decreasing rest frequency may not appear an energy-conservative strategy, the CTEH predicts that this increase in daytime active behaviours during the winter is counterbalanced by more rest during the night-time. In addition, our analyses confirmed the important role moonlight has in regulating activity patterns in *A. azarae* in our study population.

Several selective pressures, other than thermoenergetic investment, have been proposed to promote a shift to cathemeral habits in primates and other mammals. For example, individuals from a given species benefit by being day- and night-active because this may reduce resource competition and predation risk (Campera

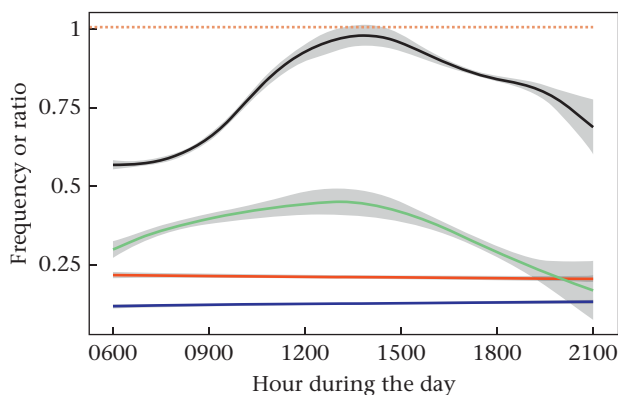


Figure 3. Daytime frequencies of travelling (red) and foraging (green) behaviours per 20 min focal observation for focal observations with resting (blue) behaviour frequencies ≤ 0.30 ($N = 3464$ focal samples, 138 individuals from 14 groups) and the temperature at the time when focal observation were taken divided by the daily maximum temperature (black), averaged over 13 years between 2001 and 2015. The lines represent the cumulative mean and the shaded areas describe the 95% confidence interval. The dashed line indicates when the daily maximum temperature was reached.

et al., 2019). Azara's owl monkeys are possibly competing for fruits with several sympatric vertebrates including black and gold howler monkeys, *Alouatta caraya*, coatis, *Nasua nasua*, and frugivorous birds (Fernandez-Duque & van der Heide, 2013). As a result, *A. azarae* may indeed benefit from utilizing different periods of the day to feed to avoid competition. Although we have never witnessed predation events of Azara's owl monkeys in our study population, a recent study of their sleeping habits suggests that monkeys may use a predator-evading strategy by changing sleeping trees nightly (Savagian & Fernandez-Duque, 2017).

Together, our results provide direct support for the CTEH and suggest that thermoenergetic demands may be critical in shaping the temporal niche of small nonhuman primates. Furthermore, our results suggest that the value of the CTEH goes beyond its ability to predict the 24 h timing of overall locomotor activity. Additionally, it represents a valuable framework to understand the 24 h distribution of complex behaviours that have opposing physiological consequences, such as moving to find and consume food versus moving to colonize a new site or find a mate. Our results also incorporate the possible effects of age and/or body size in the CTEH, as age class was a good predictor of circadian patterns of behaviour, and individuals used the day differently as they grew into adults.

Aotus have been described as having thyroid insensitivity, which has been proposed to account in part for their low metabolic rates (Whittow et al., 1979), and as such, they may be predisposed to be highly sensitive to even small variations in thermoregulatory needs (Scholander et al., 1950). Twenty-four hour biological rhythms are the result of the dual contribution of circadian clocks, which time physiological and behavioural outputs and are entrained to 24 h environmental cycles, and of the direct effect of environmental changes on each specific output known as 'masking' (Castillo-Ruiz et al., 2012; Hut et al., 2012; Smarr et al., 2013). In other words, changes in the environment, such as a sudden drop in ambient temperature, may mask the oscillations governed by the endogenous clock. Several studies have suggested that this dual regulation also shapes behaviour in *A. azarae* (Erkert et al., 2012; Fernandez-Duque et al., 2010). As we have seen in our study site, oscillations in ambient temperature can be rather stable and indeed they can act as a cycle to which endotherms could entrain their endogenous clocks (Buhr et al., 2010; Refinetti, 2015; Ruby, 2011). Although it remains to be determined whether environmental oscillations in temperature can entrain *Aotus* circadian rhythms, our results suggest that *A. azarae* integrate both long-term (weekly) stable changes in ambient temperature, which could support reliable entrainment, and short-term (hourly, daily) changes that can acutely modify behavioural outputs.

A few caveats should be taken in mind when interpreting the results of this study. First, the relationships described here do not reflect any causal effects between ambient temperatures and temporal niche shifts in the monkeys studied. Nevertheless, our study can aid in the development of hypotheses and predictions that can be tested in a controlled setting. Second, models in the set may not include key parameters that can affect energy balance and activity patterns, such as reproductive condition (e.g. mating, gestating/expecting, caretaking), solar radiation, wind velocity, food availability and predator risk, all of which induce changes in energy allocation. Third, we typically did not begin collecting focal data while animals were inactive; thus, our sampling may underestimate the amount of time spent resting by individuals. Lastly, the design of this study only enabled us to address changes in daytime activity patterns, and thus, our results do not provide any information on how night-time resting, travelling and foraging patterns may be affected by ambient temperatures or any of the other parameters in our analyses.

Other primate species can provide insight into the mechanisms regulating mammalian circadian thermoenergetics, especially those with flexible circadian behaviour, small body size and sexually dimorphic patterns of foraging behaviour. The nocturnal grey mouse lemur, *Microcebus murinus*, for example, would be an excellent model to test the CTEH, as they are highly susceptible to metabolic changes induced by changes in their environment and they have adapted well to captivity. *Microcebus murinus* are not monogamous or territorial, they are solitary foragers (Luttermann et al., 2006), females are larger than (and dominant over) males (Radespiel & Zimmermann, 2001; Thomas et al., 2015) and they use a variety of energy-saving strategies to balance their high thermoenergetic investment, including seasonal breeding (Radespiel et al., 2002), huddling (Genin et al., 2003) and daily bouts of torpor (Royo et al., 2019).

Conclusion

Our findings support the CTEH and suggest that, during seasonal thermal challenges, cathemeral Azara's owl monkeys allocate more of the daytime to behaviours that increase energy intake, potentially to compensate for the increased energetic investment in thermoregulatory needs. Further work designed to identify the physiological mechanisms and biomarkers for major changes in energy balance due to thermogenesis can provide insight into the selective pressures that may yield changes in temporal niche in owl monkeys and other mammals.

Author Contributions

J.P.P.R. and E.F.D. conceived the study and developed the theoretical framework and methodological approach. J.P.P.R. performed the analyses supported by M.C. M.C. also verified the analytical methods and the presentation and interpretation of the results. H.I. encouraged E.F.D. early on to investigate circadian thermoenergetics in the study species and provided important predictions of the hypothesis tested; he also aided in interpretation and presentation of the findings of this work. E.F.D. provided funding for the study and for J.P.P.R.'s postdoctoral position. All authors contributed to planning, performance and presentation of the analyses and to evaluation of the analytical methods and interpretation of results.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at <https://doi.org/10.1016/j.anbehav.2021.12.008>.

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Table S1

Summary of the number of focal samples used (*N*) for the analyses per group, age class, reproductive status, time of day, month, year and illuminated lunar fraction the night prior to the sample (new moon = 0.00, full moon = 1.00, presented in the table as the count per 0.10 interval)

Group	<i>N</i>	Age class	<i>N</i>	Rep. status	<i>N</i>	Time of day (hours)	<i>N</i>	Month	<i>N</i>	Year	<i>N</i>	Lunar fraction	<i>N</i>
B68	29	Adult	4095	Group	4107	0600	367	January	312	2001	127	0.00–0.10	1258
C0	294	Parentally independent	735	Solitary	878	0700	927	February	459	2002	609	0.11–0.20	629
CC	589	Parentally dependent	155			0800	657	March	230	2003	48	0.21–0.30	406
Colman	377					0900	517	April	153	2004	330	0.31–0.40	439
Corredor	156					1000	361	May	376	2005	534	0.41–0.50	338
D100	208					1100	131	June	440	2008	465	0.51–0.60	373
D1200	135					1200	45	July	897	2009	379	0.61–0.70	313
D500	939					1300	14	August	791	2010	112	0.71–0.80	382
D800	522					1400	23	September	401	2011	215	0.81–0.90	353
E350	518					1500	43	October	392	2012	313	0.91–1.00	494
E500	861					1600	224	November	312	2013	400		
F1200	130					1700	729	December	222	2014	1123		
F700	94					1800	708			2015	330		
G1300	90					1900	221						
P30	43					2000	11						
						2100	7						

We used 4985 20-minute focal samples from 140 individuals from 15 groups, collected over 13 years between 2001 and 2015.

Table S2

Model set and definitions of the parameters in each model

Model	Parameter	Definition
M1	Temperature at the hour of focal sample	Hourly temperature, as recorded by data logger, when focal sample was started, to the nearest hour
M2	Daily mean temperature	Mean recorded hourly temperature during the 24 h period when focal sample was taken
M3	Daily minimum temperature	Lowest recorded hourly temperature during the 24 h cycle when focal sample was taken
M4	Daily maximum temperature	Highest recorded hourly temperature during the 24 h cycle when focal sample was taken
M5	Daily temperature range	Difference between daily maximum temperature and the daily minimum temperature
M6	Daily hours below 10 °C	Number of hours when temperatures were measured below 10 °C during the 24 h cycle when focal samples were taken
M7	Daily hours below 5 °C	Count of hours when temperatures were measured below 5 °C during the 24 h cycle when focal sample was taken
M8	Weekly mean temperature	Mean of hourly temperature in the 7 days preceding the date of the focal sample
M9	Weekly minimum temperature	Lowest recorded hourly temperature 7 days preceding the date of the focal sample
M10	Weekly maximum temperature	Highest recorded hourly temperature in the 7 days preceding the date of the focal sample
M11	Weekly temperature range	Difference between weekly maximum temperature and the weekly minimum
M12	Weekly count hours below 10 °C	Number of recorded hourly temperatures below 10 °C in the 7 days preceding the date of the focal sample
M13	Weekly count hours below 5 °C	Number of recorded hourly temperatures below 5 °C in the 7 days preceding the date of the focal sample

Model	Parameter	Definition
M14	Moon fraction illuminated	Lunar fraction illuminated on the night prior to when focal samples were taken (new moon = 0.00, full moon = 1.00)
M15	Age class	Nutritionally dependent infants (≤ 6 months of age), nutritionally independent juveniles and subadults (1–4 years of age) or adults (5+ years of age; solitaries and members of a group)
M16	Reproductive status	If individual was an adult member of a group or living solitarily
M17	Index of the daily maximum	Temperature at the hour of focal sample divided by the daily maximum temperature (0.00–1.00). Indicates how close the temperature was when monkeys were sampled to the daily maximum temperature (M1/M4)
M18	Photoperiod	Number of minutes between sunrise and sunset during the 24 h cycle when focal samples were collected
M19	Temp. at focal*moon fraction	Interaction between temperature at the hour of focal sample and the moon fraction illuminated (M1*M14)
M20	Temp. at focal*age class	Interaction between the temperature at the hour of focal sample and the focal animal's assigned age class (M1*M15)
M21	Temp. at focal*rep. status	Interaction between the temperature at the hour of focal sample and the focal animal's assigned reproductive status (M1*M16)
M22	Daily mean temp.*moon fraction	Interaction between the daily mean temperature and moon fraction illuminated (M2*M14)
M23	Daily mean temp.*age class	Interaction between the daily mean temperature and the focal animal's assigned age class (M2*M15)
M24	Daily mean temp.*rep. status	Interaction between the daily mean temperature and the focal animal's assigned reproductive status (M2*M16)
M25	Daily min. temp.*moon fraction	Interaction between the daily minimum temperature and the moon fraction illuminated (M3*M14)
M26	Daily min. temp.*age class	Interaction between the daily minimum temperature and the focal animal's assigned age class (M3*M15)

Model	Parameter	Definition
M27	Daily min. temp.*rep. status	Interaction between the daily minimum temperature and the focal animal's assigned reproductive status (M3*M16)
M28	Daily max. temp.*moon fraction	Interaction between the daily maximum temperature and the moon fraction illuminated (M4*M14)
M29	Daily max. temp.*age class	Interaction between the daily maximum temperature and the focal animal's assigned age class (M4*M15)
M30	Daily max. temp.*rep. status	Interaction between the daily maximum temperature and the focal animal's assigned reproductive status (M4*M16)
M31	Daily temp. range*moon fraction	Interaction between the daily temperature range and the moon fraction illuminated (M5*M14)
M32	Daily temp. range*age class	Interaction between the daily temperature range and the focal animal's assigned age class (M5*M15)
M33	Daily temp. range*rep. status	Interaction between the daily temperature range and the focal animal's assigned reproductive status (M5*M16)
M34	Daily hours < 10 °C*moon fraction	Interaction between the daily hours below 10 °C and the moon fraction illuminated (M6*M14)
M35	Daily hours < 10 °C*age class	Interaction between the daily hours below 10 °C and the focal animal's assigned age class (M6*M15)
M36	Daily hours < 10 °C*rep. status	Interaction between the daily hours below 10 °C the focal animal's assigned reproductive status (M6*M16)
M37	Daily hours < 5 °C*moon fraction	Interaction between the daily hours below 5 °C and the moon fraction illuminated (M7*M14)
M38	Daily hours < 5 °C*age class	Interaction between the daily hours below 5 °C and the focal animal's assigned age class (M7*M15)
M39	Daily hours < 5 °C*rep. status	Interaction between the daily hours below 5 °C the focal animal's assigned reproductive status (M7*M16)

Model	Parameter	Definition
M40	Weekly mean temp.*moon fraction	Interaction between the weekly mean temperature and the moon fraction illuminated (M8*M14)
M41	Weekly mean temp.*age class	Interaction between the weekly mean temperature and the focal animal's assigned age class (M8*M15)
M42	Weekly mean temp.*rep. status	Interaction between the weekly mean temperature and the focal animal's assigned reproductive status (M8*M16)
M43	Weekly min. temp.*moon fraction	Interaction between the weekly minimum temperature and the moon fraction illuminated (M9*M14)
M44	Weekly min. temp.*age class	Interaction between the weekly minimum temperature and the focal animal's assigned age Class (M9*M15)
M45	Weekly min. temp.*rep. status	Interaction between the weekly minimum temperature and the focal animal's assigned reproductive status (M9*M16)
M46	Weekly max. temp.*moon fraction	Interaction between the weekly maximum temperature and the moon fraction illuminated (M10*M14)
M47	Weekly max. temp.*age class	Interaction between the weekly maximum temperature and the focal animal's assigned age class (M10*M15)
M48	Weekly max. temp.*rep. status	Interaction between the weekly maximum temperature and the focal animal's assigned reproductive status (M10*M16)
M49	Weekly temp. range*moon fraction	Interaction between the weekly temperature range and moon fraction illuminated (M11*M14)
M50	Weekly temp. range*age class	Interaction between the weekly temperature range and the focal animal's assigned age class (M11*M15)
M51	Weekly temp. range*rep. status	Interaction between the weekly temperature range and the focal animal's assigned reproductive status (M11*M16)
M52	Weekly hours < 10 °C*moon fraction	Interaction between the weekly hours below 10 °C and the moon fraction illuminated (M12*M14)

Model	Parameter	Definition
M53	Weekly hours < 10 °C*age class	Interaction between the weekly hours below 10 °C and the focal animal's assigned age class (M12*M15)
M54	Weekly hours < 10 °C*rep. status	Interaction between the weekly hours below 10 °C and the focal animal's assigned reproductive status (M12*M16)
M55	Weekly hours < 5 °C*moon fraction	Interaction between the weekly hours below 5 °C and the moon fraction illuminated (M13*M14)
M56	Weekly hours < 5 °C*age class	Interaction between the weekly hours below 5 °C and the focal animal's assigned age class (M13*M15)
M57	Weekly hours < 5 °C*rep. status	Interaction between the weekly hours below 5 °C and the focal animal's assigned reproductive status (M13*M16)
M58	Index of the daily maximum*moon fraction	Interaction between the index of the daily maximum and the moon fraction illuminated (M17*M14)
M59	Index of the daily maximum*age class	Interaction between the index of the daily maximum and the focal animal's assigned age class (M17*M15)
M60	Index of the daily maximum*rep. status	Interaction between the index of the daily maximum and the focal animal's assigned reproductive status (M17*M16)
M61	Photoperiod*moon fraction	Interaction between the photoperiod and the moon fraction illuminated (M18*M14)
M62	Photoperiod*age class	Interaction between the photoperiod and the focal animal's assigned age class (M18*M15)
M63	Photoperiod*rep. status	Interaction between the photoperiod and the focal animal's assigned reproductive status (M18*M16)
M64	Photoperiod*daily mean temp.	Interaction between the photoperiod and the daily mean temperature (M18*M2)
M65	Photoperiod*daily min. temp.	Interaction between the photoperiod and the daily minimum temperature (M18*M3)
M66	Photoperiod*daily max. temp.	Interaction between the photoperiod and the daily maximum temperature (M18*M4)
M67	Photoperiod*daily temp. range	Interaction between the photoperiod and the daily maximum temperature (M18*M5)
M68	Photoperiod*daily hours < 10 °C	Interaction between the photoperiod and the daily hours below 10 °C (M18*M6)

Model	Parameter	Definition
M69	Photoperiod*daily hours < 5 °C	Interaction between the photoperiod and the daily hours below 5 °C (M18*M7)
M70	Photoperiod*weekly mean temp.	Interaction between the photoperiod and the weekly mean temperature (M18*M8)
M71	Photoperiod*weekly min. temp.	Interaction between the photoperiod and the weekly minimum temperature (M18*M9)
M72	Photoperiod*weekly max. temp.	Interaction between the photoperiod and the weekly maximum temperature (M18*M10)
M73	Photoperiod*weekly temp. range	Interaction between the photoperiod and the weekly temperature range (M18*M11)
M74	Photoperiod*weekly hours < 10 °C	Interaction between the photoperiod and the weekly hours below 10 °C (M18*M12)
M75	Photoperiod*weekly hours < 10 °C	Interaction between the photoperiod and the weekly hours below 5 °C (M18*M13)
M76	Photoperiod*weekly hours < 10 °C	Interaction between the photoperiod and the weekly hours below 5 °C (M18*M14)
M77	Photoperiod*index of the daily maximum	Interaction between the photoperiod and the index of the daily maximum (M18*M17)

Outcome variables of interest were fitted to 77 linear models, consisting of either a single parameter or the interaction between two parameters. Linear mixed models were used to estimate the fit of the data to each of the models in the set; crossed random effect variables included group name and the focal animal's unique identification code/name.

Table S3

Best-fit models for frequencies of resting, travelling, and foraging per 20 min focal sample ($N = 4985$, 140 individuals, 13 years sampled between 2001 and 2015)

Outcome variable	Model	Model parameters	K	AICc	Δ AICc	AICc weight	Cum. AICc weight	Ev. ratio	LL
Frequency of resting	M42	Weekly mean temp.*rep. status	7	-6778.87	0	0.64	0.64	1	3396
	M24	Daily mean temp.*rep. status	7	-6775.47	3	0.12	0.75	5	3395
	M40	Weekly mean temp.*moon fraction	7	-6774.75	4	0.09	0.84	7	3395
	M8	Weekly mean temp.	5	-6773.57	5	0.05	0.89	14	3396
	M41	Weekly mean temp.*age class	9	-6773.73	5	0.04	0.93	14	3393
	M30	Daily max. temp.*rep. status	7	-6772.22	7	0.02	0.96	28	3393
	M70	Photoperiod*weekly mean temp	7	-6771.22	8	0.01	0.97	45	3393
	M21	Temp. at focal*rep. status	7	-6771.27	9	0.01	0.98	102	3392
Frequency of travelling	M29	Daily max. temp.*age class	9	-9520	0	0.45	0.45	1	4769
	M41	Weekly mean temp.*age class	9	-9519	1	0.28	0.73	2	4768
	M30	Daily max. temp.*rep. status	7	-9517	3	0.10	0.83	5	4765
	M28	Daily max. temp.*moon fraction	7	-9515	4	0.05	0.88	8	4765
	M40	Weekly mean temp.*moon fraction	7	-9515	5	0.05	0.93	10	4762
	M4	Daily max. temp.	5	-9513	6	0.02	0.95	23	4763
	M42	Weekly mean temp.*rep. status	7	-9513	7	0.01	0.96	33	4765
	M47	Weekly max. temp.*age class	9	-9512	7	0.01	0.97	40	4762

Outcome variable	Model	Model parameters	<i>K</i>	AICc	Δ AICc	AICc weight	Cum. AICc weight	Ev. ratio	LL
Frequency of foraging	M48	Weekly max. temp.*rep. status	7	-9511	8	0.01	0.98	58	4763
	M8	Weekly mean temp.	5	-9511	8	0.01	0.98	68	4761
	M46	Weekly max. temp.*moon fraction	7	-9511	9	0.01	0.99	73	4763
	M10	Weekly max. temp.	5	-9509	10	0.00	0.99	123	4760
	M41	Weekly mean temp.*age class	9	-7119	0	0.49	0.49	1	3568
	M70	Photoperiod*weekly mean temp.	7	-7118	1	0.32	0.81	2	3566
	M40	Weekly mean temp.*moon fraction	7	-7115	3	0.10	0.90	5	3565
	M8	Weekly mean temp.	5	-7115	4	0.08	0.8	6	3563
	M42	Weekly mean temp.*rep. status	7	-7112	7	0.02	1.00	32	3563

Crossed random effect variables included the focal animal’s group name and unique identification code. The parameters for each model are presented, as well as the number of parameters in the model (*K*), the values for Akaike’s corrected information criterion (AICc) and the difference between each model and the best-fit model (Δ AICc), the Akaike weight for each model, and the cumulative weight, evidence ratio and log likelihood (LL).