

Paternal Activity Budgets of the Peruvian San Martín Titi Monkey (*Plecturocebus oenanthe*) in Response to Habitat Destruction, Seasonality, Thermal Stress, and Infant Care

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Abstract: Primates face a range of energetic challenges, including limited resources, thermal stress, and infant care, which fluctuate with climate and season. Some primates manage stressors by adopting energy maximizing or time minimizing strategies, leading to significant changes in behavior across climatic and reproductive seasons. Anthropogenic activities can amplify such costs by reducing available resources, which may restrict the ability to meet nutritional needs or encourage risky behaviors to compensate such as foraging on crops or foods stored by people (anthropogenic foraging). For this reason, it is crucial to examine how primates cope with anthropogenic sources of stress in addition to natural ones. I examined time allocation decisions of adult male caregivers in San Martín titi monkeys (*Plecturocebus oenanthe*) to see if males adopt a time minimizing strategy and increase their time resting in response to a higher level of habitat destruction, during the dry season, at elevated daily temperatures, and with younger infants. I expected opposite outcomes for traveling, feeding, and socializing. I monitored the activity budgets of two *P. oenanthe* adult males over 11 months using instantaneous sampling and analyzed data with generalized linear mixed models. In support of my hypothesis, less time was spent in energetically demanding behaviors in response to habitat destruction, temperature, and infant age, characterizing them as time minimizers. I further observed that habitat destruction was positively associated with anthropogenic foraging, putting individuals at risk of disease, injury, and death. Given these results, conservation strategies should focus on protecting extensive areas of forest, improving habitat connectivity, and reducing the exposure of titi monkeys to anthropogenic areas.

Key words: Habitat loss, thermoregulation, parental care, anthropogenic foraging

Introduction

A range of ecological factors can affect primate activity budgets, and the way that primates allocate time to daily activities can greatly affect their ability to survive and reproduce (Coelho 1986; DeFler 1995). Under natural conditions, primates cope with the energetic costs arising from seasonal fluctuations in food availability (dispersion, abundance), ambient temperature, and the need for infant care. Habitat destruction can increase these existing demands by reducing access to resources and altering local climate patterns. Clarifying how primates cope with anthropogenic habitat disturbance in addition to naturally occurring ecological demands can lead to improvements in the development of conservation strategies.

The availability and quality of food resources are known to be the most important ecological factors affecting primate behavior since they entail a tradeoff between energy acquisition and expenditure (Knott 1999; Chaves *et al.* 2011; Chapman *et al.* 2015; Lambert and Rothman 2015). In addition, ambient temperature has been shown to significantly influence behavior as primates attempt to balance thermoregulation and energy intake in response to climatic conditions (Kamilar and Beaudrot 2018). The two main drivers of variation in food resources and thermal stress are habitat destruction (Arroyo-Rodríguez and Mandujano 2006; Chapman *et al.* 2006; Arroyo-Rodríguez *et al.* 2017) and seasonality (Murphy and Lugo 1995; Bunker and Carson 2005), which can lead to major fluctuations in ecological pressures (Thompson *et al.* 2014; Chapman *et al.* 2015; Charpentier *et al.* 2018).

Shifts in resource availability and quality represent critical challenges for primates, and some species cope by adopting energy maximizing or time minimizing approaches. Originally proposed by Schoener (1971), this model claims that energy maximizers attempt to obtain the maximum amount of energy during the available foraging time (Hixon 1982) by foraging and feeding for as long as possible. For instance, in periods of seasonal scarcity when preferred foods were less available, François' langurs (*Trachypithecus francoisi*) (Zhou *et al.* 2007) and Gursky's spectral tarsier (*Tarsius spectrumgurskyae*) (Gursky 2000) followed an energy maximizing strategy by increasing the proportion of time spent foraging, supplementing their diet with alternative foods, and reducing rates of resting and socializing.

In contrast, time minimizers prioritize energy conservation and forage and feed only until they meet their net metabolic requirements. For example, bearded saki monkeys (*Chiropotes satanas chiropotes*) living in 1-ha, 10-ha, and 100-ha forest fragments traveled less and rested more than those in continuous forest (Boyle and Smith 2010), indicating time minimization. Similar alterations to activity have been shown in diademed sifakas (*Propithecus diadema*) living in fragmented forest compared with those living in continuous forest (Irwin 2008). Primates may employ similar activity budgeting in response to lower food abundance and quality in the dry season by limiting costly behaviors, such as traveling and foraging, and increasing time spent inactive and socializing. This has been observed in San Martín titi monkeys (*Plecturocebus oenanthe*) (DeLuycker 2007), buffy-headed marmosets (*Callithrix flaviceps*) (Ferrari and Hilário 2014), and black-fronted titi monkeys (*Callicebus nigrifrons*) (Nagy-Reis and Setz 2017). Time minimizing has also been used by primates to thermoregulate when exposed to extreme temperatures. For example, as temperatures become warmer black howler monkeys (*Alouatta pigra*) rest more often (Aristizabal *et al.* 2018), Barbary macaques (*Macaca sylvanus*) (Majolo *et al.* 2013) feed less, while chimpanzees (*Pan troglodytes*) (Koshelev and Anderson 2009) and southern muriquis (*Brachyteles arachnoides*) (Talebi and Lee 2010) increase resting and decrease time spent feeding.

Infant care also represents a significant energetic challenge for caregivers. For female primates, lactation is the most expensive activity in terms of caloric demands (Clutton-Brock 1991). Mothers cope with reproductive costs by altering diet, such as by increasing the quality or quantity of foods (McCabe and Fedigan 2007; Murray *et al.* 2009), or by adjusting time allocation decisions to either maximize or conserve energy (Rose 1994; Lappan 2009; Dunham and Rodriguez-Saona 2018). Females may intensify their use of such strategies as resources become scarcer due to habitat destruction or seasonal changes. For instance, a study on red colobus (*Procolobus rufomitratus*) living in logged and old-growth forest found that females in logged areas compensated for a loss of resources by following an energy maximizing approach (Milich *et al.* 2014). They did this by adopting a more varied diet with a higher proportion of readily available,

but less-preferred and possibly lower-quality, food items. Compared with females in old-growth habitat, they also devoted more time to feeding and less time to all other activities. These behavioral changes allowed female *P. rufomitratus* living in logged areas to maintain similar densities to those in old-growth forest.

After lactation, infant transport is the next most costly form of infant care (Altmann and Samuels 1992) and is the typical way that male primates contribute to infant care (Kleiman 1985; Wright 1990). In species with substantial male care, adult males provide the bulk of infant transportation and dedicate proportionally more time to infant care than other group members (Kleiman 1985; Fernandez-Duque *et al.* 2009; Storey and Ziegler 2016). In several species with obligate paternal care, fathers invest significantly more time providing care at the earliest stages of infant development (Wright 1984; Price 1992a; Rotundo *et al.* 2005). For instance, adult male dusky titi monkeys (*Plecturocebus moloch*) allocate >90% of their time to infant care during the first two months of life, which gradually declines (40-60%) by three to four months of age (Wright 1990). Paternal care costs are evident in loss of time and also disruption of daily activities such as foraging and traveling. For example, infant carrying diminished insect foraging success of fathers in *P. moloch* (see Wright 1984), and lowered feeding rates of *P. oenanthe* fathers (see DeLuycker 2007). In captive cotton-top tamarins (*Saguinus oedipus*), greater infant body mass and longer durations of carrying reduced travel speeds in adults (Caperos *et al.* 2012).

For species with considerable male care it is important to understand how adult males adapt behaviorally to socioecological stressors, since this may affect infant care and development as has been seen in studies on maternal care (Lee *et al.* 1991; Dunbar *et al.* 2002; Maestripieri *et al.* 2009; Milich *et al.* 2014). Since mothers experience the added demands of gestation and lactation it cannot be assumed that paternal and maternal responses will be equivalent. There has been a lack of research on paternal responses to seasonal and parental sources of stress, and no studies thus far have examined the impacts of habitat destruction on male activity in primates with obligate paternal care. *Plecturocebus oenanthe*, endemic to premontane tropical forests in the San Martín region of Peru, is an ideal species for a study of the co-occurring effects of habitat destruction, thermal stress, seasonality, and infant care on paternal activity budgets. It suffers from varying degrees of habitat degradation and fragmentation (Shanee *et al.* 2013) and climatic seasons are strongly demarcated by variation in food availability and temperature (DeLuycker 2007, 2012). The adult males are the principal infant carriers, and DeLuycker (2007, 2014) showed that infant carrying was associated with changes in their daily activity patterns.

I examined whether *P. oenanthe* adult males employ either energy maximizing or time minimizing strategies to cope with the demands of infant care under various environmental stressors. Building on prior titi monkey research (DeLuycker 2007; Souza-Alves 2013; Nagy-Reis and Setz 2017), I examined whether adult male *P. oenanthe* adopt a time minimizing

approach in response to elevated energetic burdens. Specifically, I investigated the effects of habitat destruction, tropical season, daily temperature range, and infant age (a proxy for infant care costs). I predicted that resting (including social rest) would increase in response to a higher level of habitat destruction, in the dry season, with greater daily temperature ranges, and with younger infant ages. I expected the opposite outcomes for traveling, feeding, and social interaction.

Methods

Study sites

This study took place in the San Martín region of north-eastern Peru (Fig. 1) over 11 months during two field seasons—from July to December 2015 and from August 2016 to January 2017. I collected data on adult males living in two different premontane tropical forest fragments (Holdridge 1967). Sites were previously assessed (manuscript in review) for relative level of habitat destruction (hereafter HD), and I designated these as either lower or higher HD sites. The lower HD site was near the town of Yantaló (5°59'21.64"S, 77°2'42.96"E) at an elevation of 868 m. The higher HD site was near the village of Calzada (6°2'47.18"S, 77°5'58.92"E) at 820 m. The lower HD site was 4.15 ha, nearly twice the size of the higher HD site (2.15 ha). Tree density (32.9 vs.

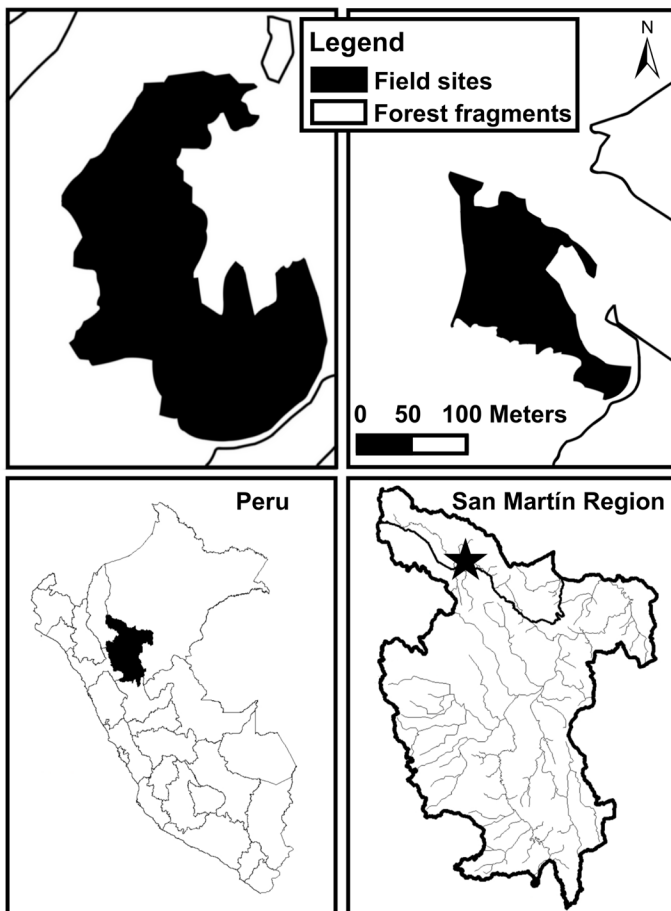


Figure 1. Field sites (top left: lower HD site; top right: higher HD site) and their location in the San Martín region (bottom right) of Peru (bottom left).



Figure 2. Adult male carrying an infant (3.5 months old) at Yantaló. Photo by Shannon Hodges.



Figure 3. Adult male carrying an infant (1 month old) at Calzada. Photo by Shannon Hodges.

15.5 m²/100 m²) and fruit availability per individual (1.74 vs 1.46 m²/100 m²) were significantly reduced at the higher compared with the lower HD site. Crop fields of mainly plantains, rice, and coffee surrounded both forest fragments. Domesticated dogs roamed the area and entered the forest at the higher HD site daily, but rarely did so at the lower HD site.

Study species and groups

The small *P. oenanthe* (~1.0 kg) inhabits premontane tropical forest at maximum elevations of approximately 1,129 m (Bóveda-Penalba *et al.* 2009). It eats mainly fruits and insects, supplementing its diet with new leaves, flowers, and seeds (DeLuycker 2007, 2012). Fathers carry infants within 24 hours of their birth and are the primary infant caregivers and attachment figures (DeLuycker 2007, 2014). I collected data on the activity budgets of the resident adult male of each study group (N = 2). I compared body size, fur length and color, facial mask development, and visually identified genitalia to determine the age and sex class of all study group individuals (DeLuycker 2007). Since I did not confirm genetic

paternity of infants, I refer to subjects as “males” rather than “fathers.”

In both groups, males cared for one infant per field season. The adult male (Fig. 2) at the lower HD site (Yantaló) lived with an adult female and a juvenile female (classed as a subadult in the second season). The infant observed in the first field season was missing in the second season and may have either died or been captured for the illegal pet trade, which had occurred previously at this site according to a local farmer. The adult male (Fig. 3) at the higher HD site (Calzada) resided with an adult female, one subadult female that was absent in the second field season, a subadult male, and a juvenile female (classed as a subadult in the second season). The infant born in the first season was classed as a juvenile the following year.

Activity budget data collection

I trained two field assistants to help with behavioral data collection, Daniel Morales Rodríguez and Raul Saucedo Quispe, and verified that we achieved consistent agreement on the individual identity and activity category designations prior to formal data collection. Assistants worked in different field seasons, therefore I used the index of concordance (Martin and Bateson 2007) to test for interobserver reliability between my observations and each of theirs in 30-minute parallel observation training sessions (Daniel: 93.33%, $N = 10$; Raul: 96%, $N = 10$). We collected activity budget data and sorted behaviors into the categories of rest, travel, feed, social interaction, and other (Table 1). Behaviors classified as other occurred too infrequently (3% of budget) to be analyzed in this study. During daily focal follows, we tracked males while they cared for infants (for example, carrying, crouching over, retrieving, grooming, and cleaning) and used instantaneous focal sampling to collect data every two minutes (Altmann 1974). The size of the dataset was limited by the paternal care rate of study subjects since we did not consistently monitor males when they were not engaging in infant care.

For each data point, we recorded the relative level of HD for each study site (lower or higher based on prior research). I classified tropical seasons as dry (May–September) or wet (October–April), and calculated daily temperature range in degrees Celsius ($^{\circ}\text{C}$) based on climate data retrieved from the National Meteorology and Hydrology Service of Peru (SENAMHI 2017). Infant age in months functioned as a proxy of infant care costs since infant care is considered to be potentially incompatible with certain activities such as

foraging and traveling (Price 1992b; DeLuycker 2007; Caperos *et al.* 2012) and is physically demanding for small Neotropical primates (Tardif 1994; Sánchez *et al.* 1999; Achenbach and Snowdon 2002). To control for the effects of time of day, I classified diurnal periods as morning (prior to 11:00), midday (11:00–13:00), or afternoon (after 13:00). We tracked weather conditions under the categories of no rain, light rain, or heavy rain. Study subjects always rested during heavy rain, so I removed observations recorded during this weather to control for its impact on behavior.

To improve dataset reliability, I removed instantaneous data points for those days during which fewer than 20 minutes of focal follow observation were recorded. Infant age ranged from 0–6 months during the field study. Prior to analysis, I also excluded observations months 5 and 6 due to insufficient data collected on activity budgets. I used R Studio (R Development Core Team 2017) to transform and analyze all data. After data cleanup, instantaneous data totaled 7,069 sample points (243.5 hours) collected on 96 focal follow days. I transformed data prior to analysis by calculating activity percentages for each category-based level of HD, season, daily temperature range, infant age, time of day, and day of observation. I calculated sample percentages ($N = 172$ per behavior category) by dividing the sum of instantaneous data points per activity by the total number of points recorded and multiplying these by 100 (package `dplyr`).

Statistical analysis

I used generalized linear mixed models (GLMMs) with package `lme4` to examine my predictions. I created separate models for each behavior category (rest, travel, feed, and social interaction) and used activity percentages as the response variable. Fixed effects included level of HD, season, daily temperature range, and infant age. I coded time of day as a random effect and included sample number (1–172) as an observation level random effect to minimize overdispersion (Xavier 2014). I fit models with a binomial error distribution and logit link, and estimated parameters using maximum likelihood for model comparison (Bolker *et al.* 2009). Instantaneous observation counts provided weights for percentage samples.

I built GLMMs ranging from intercept-only (null) to full interaction models, keeping the same random effects in each model. I used variance inflation factor (VIF) estimates to assess multicollinearity among fixed effects (package `car`) and discarded models with $\text{VIFs} \geq 4.0$ (Zuur *et al.*

Table 1. Ethogram of adult male San Martin titi monkeys (*Plecturocebus oenanthe*).

Activity	Definition
Rest	A period of inactivity, including sitting, standing, lying down, huddling, and self-grooming
Travel	To move from one location to another, including walking, running, climbing, or leaping
Feed	To search for, chew, or swallow food items
Social	Dyadic interactions, including playing, allogrooming, or engaging in agonistic or sexual activity
Other	Engaging in infrequent behaviors that did not otherwise fall into other categories, such as vocalizing and scent-marking

Table 2. Summary of activity model comparisons of adult male activity proportion.

Activity models	ΔAICc	Likelihood ratio tests		
		χ^2	df	P-value
Rest (N = 169)				
HD + Season + Temperature + Age	0.19	–	–	–
HD + Temperature + Age	0.00	1.99	1	0.1582
HD + Age	10.36	12.52	1	0.0004*
Age	22.87	14.63	1	0.0001*
Intercept	46.33	25.56	1	<0.0001*
Travel (N = 163)				
HD + Season + Temperature + Age	2.10	–	–	–
HD + Temperature + Age	0.00	0.08	1	0.7782
HD + Age	2.29	4.45	1	0.0349*
Age	15.24	15.08	1	0.0001*
Intercept	63.61	50.46	1	<0.0001*
Feed (N = 171)				
HD + Season + Temperature + Age	0.58	–	–	–
Season + Temperature + Age	0.00	1.60	1	0.2058
Temperature + Age	0.57	2.72	1	0.0994
Temperature	3.95	5.51	1	0.0189*
Intercept	15.95	14.10	1	0.0002*
Social (N = 172)				
HD + Season + Temperature + Age	5.39	–	–	–
HD + Temperature + Age	3.28	0.07	1	0.7860
HD + Age	1.24	0.10	1	0.7549
HD	0.00	0.88	1	0.3470
Intercept	3.35	5.45	1	0.0196*

Activity budget models fit by relative level of habitat destruction, season, daily temperature range, and infant age. Likelihood ratio test results indicate whether a simpler model is preferred (null hypothesis) compared to the next most complex model (i.e. compared in ascending order of complexity). *Significant *P*-values. Bolded terms indicate best fitting models indicated by ΔAICc (<10.0) and likelihood ratio tests ($P < 0.05$).

2010). Several of the interaction models failed to converge, likely due to small sample size, and I discarded these. For the remaining GLMMs, I explored the data to verify that they met model assumptions. I identified highly influential outliers using Cook's distance with package stats and used 2.0 as a cutoff value. Next, I refit models after removing the most severe outliers for each activity category, ensuring that categorical behavior models used the same dataset. I discarded all interaction models either due to convergence or multicollinearity issues.

To initially evaluate models, I calculated the difference between delta AICc (ΔAICc) values (package aods3) and considered models with $\Delta\text{AICc} \geq 10.0$ to be implausible (Burnham and Anderson 2002). Next, I compared nested models. I identified best fitting models using χ^2 likelihood ratio tests ($\alpha = 0.05$) in package stats (Anderson *et al.* 2000; Bolker *et al.* 2009). In the interest of full reporting, I refit both the best and full models using restricted maximum likelihood estimation (REML) and carried out Wald χ^2 tests of fixed effects with package glmmTMB ($\alpha = 0.05$) (Bolker *et al.* 2009). I reported effect sizes as odds ratio estimates. Level of HD odds ratios specified the odds of each type of activity occurring at the higher HD site compared with odds at the lower HD site. Season odds ratios indicated the odds of

activity during the wet season compared with the dry season. Odds ratios for temperature and infant age (in months) indicate the change in odds of each activity per one unit increase in $^{\circ}\text{C}$ and month, respectively. I generated box plots of data used in GLMMs with package ggplot2. I carried out *post-hoc* examinations of feeding percentages across levels of HD and seasons to investigate foraging on crops or foods that people have stored (anthropogenic foraging). To do this, I categorized instantaneous feeding observations as either anthropogenic or natural, and then carried out χ^2 tests to evaluate differences in feeding bout type holding either level of HD or season ($\alpha = 0.05$) constant.

Data availability

The datasets analyzed during the study are available from the author on reasonable request.

Results

Activity models and tests of fixed effects

Table 2 shows the results of model comparisons based on ΔAICc and χ^2 likelihood ratio testing. The model with level of HD, daily temperature range, and infant age fitted the resting and traveling data best. The two-term model with level of

Table 3. Tests of fixed effects for best fitting and full models of adult male activity.

	Effect size	Wald tests of fixed effects		
Best and full models	Odds ratio	χ^2	df	P-value
Rest (N = 169)				
HD	1.70	13.05	1	0.0003*
Temperature	1.12	11.80	1	0.0006*
Age	0.69	27.83	1	<0.0001*
HD	1.82	14.91	1	0.0001*
Season	1.36	1.83	1	0.1763
Temperature	1.11	12.65	1	0.0004*
Age	0.67	29.35	1	<0.0001*
Travel (N = 163)				
HD	0.64	13.45	1	0.0002*
Temperature	0.95	4.26	1	0.0391*
Age	1.55	63.42	1	<0.0001*
HD	0.65	11.65	1	0.0006*
Season	1.05	0.07	1	0.7847
Temperature	0.95	4.09	1	0.0431*
Age	1.54	53.78	1	<0.0001*
Feed (N = 171)				
Temperature	0.87	12.52	1	0.0004*
Age	1.21	4.99	1	0.0255*
HD	0.80	1.29	1	0.2563
Season	0.59	3.46	1	0.0629
Temperature	0.86	13.54	1	0.0002*
Age	1.29	7.75	1	0.0054*
Social (N = 172)				
HD	0.58	4.66	1	0.0308*
HD	0.61	3.47	1	0.0626
Season	0.90	0.58	1	0.4454
Temperature	1.11	0.07	1	0.7856
Age	0.99	0.08	1	0.7840

Fixed effects tests of model terms using restricted maximum likelihood estimation (REML).
*Significant P-values. Best fitting models are shown first and bolded.

temperature and infant age predicted feeding better than other models, though $\Delta AICc$ and χ^2 testing indicated that the model including season also fit the data adequately as well ($\Delta AICc = 0.00$, $P = 0.0994$). Level of HD was the only term included in the best fitting model of social interaction. Models with fixed effects were typically much more plausible than intercept-only models, which had $\Delta AICc$ values that were several times larger than those of the main effects GLMMs.

Table 3 shows the odds ratio estimates and Wald χ^2 tests of fixed effects results. All terms in the best fitting models were significant ($P < 0.05$). According to the best model, odds of rest increased with a higher level of HD and greater daily temperature ranges and decreased with each increase in month

of infant age. Similarly, only level of HD, daily temperature range, and infant age had statistically significant impacts in the full model of rest. Resting was non-significantly more likely to occur in the wet than in the dry season, as shown by the odds ratio estimate. In the best fitting traveling model, odds decreased with a higher level of HD and greater daily temperature ranges and increased with infant age. The full model indicated that odds of traveling were non-significantly higher during the wet compared with the dry season. Similarly, for both best fitting and full models of feeding, the odds were lower with more extreme temperature ranges and higher as infants grew older. Odds of feeding were non-significantly greater at the higher compared with the lower HD site, and

greater in the dry than in the wet season. Finally, the best fitting model indicated that the odds of social interaction were more likely at the lower than at the higher HD site. According to the full model, odds of socializing were non-significantly more likely during the wet season and decreased with larger temperature ranges and older infant ages. Figure 4 displays data used in GLMMs as box plots of mean proportion of time per day allocated to activities by level of HD, season, mean daily temperature range, and infant age.

Post-hoc tests of foraging

According to chi-squared tests, anthropogenic foraging (Fig. 5 and Fig. 6) took place significantly more often at the higher HD site compared with the lower HD site ($\chi^2 = 5.46$, $df = 1$, $P = 0.0194$). At the higher HD site, this type of foraging accounted for 2.91% of instantaneous feeding observations versus 0.84% of feeding observations at the lower HD site. There were no statistically significant differences in anthropogenic foraging across seasons ($\chi^2 = 0.19$, $df = 1$, $P = 0.4716$).

Discussion

The results provide strong support for the hypothesis that *P. oenanthe* males followed a time minimizing strategy to cope with elevated energetic demands that resulted from habitat destruction, thermal stress, and infant care, but not in response to seasonality. As expected, I found that a greater degree of habitat destruction was significantly associated with higher percentages of resting and lower percentages of traveling and socializing. These results concur with prior research showing that titi monkeys employ a time minimization to cope with lower food availability due to habitat destruction. For instance, research by Souza-Alves (2013) on Coimbra-Filho's titi monkeys (*Callicebus coimbrai*) showed that individuals living in a smaller forest fragment (14 ha) spent significantly less time traveling and feeding than those living in a larger area (522 ha). The smaller fragment group also spent more time resting and socializing, though intergroup differences were not significant. Similar energy-conserving

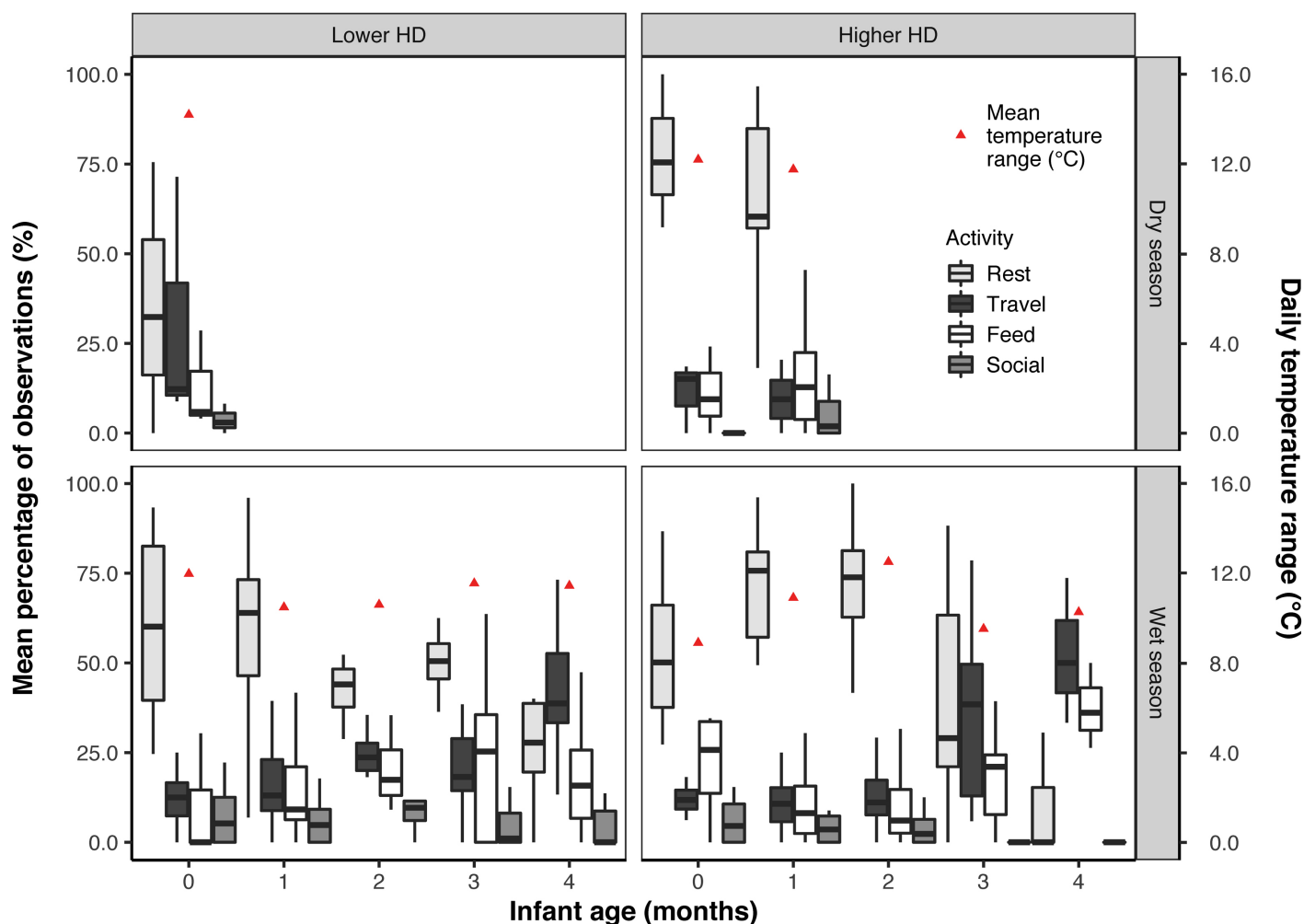


Figure 4. Mean percentage of time that adult males devoted to each activity by relative level of habitat destruction (HD), season, mean daily temperature range (°C), and infant age (months) (N = 172 percentage samples).



Figure 5. Adult female (left) and subadult female (right) feeding on cultivated plantains 9 m from the forest edge in Yantaló. Photo by Shannon Hodges.



Figure 6. Adult male (background), carrying an infant (2.6 months old), and subadult male (foreground) exploring a shack where plantains are stored. Photo by Shannon Hodges.

responses to habitat destruction have been found in primates with a range of dietary needs, including folivores (*Colobus vellerosus*: Wong and Sicotte 2007; *Alouatta palliata*: Dunn *et al.* 2009; *Chlorocebus djamdjamentis*: Mekonnen *et al.* 2017), frugivores (*Ateles geoffroyi*: Chaves *et al.* 2011), and seed predators (*C. satanas chiropotes*: Boyle *et al.* 2009; Silva and Ferrari 2009).

Contrary to my prediction, feeding did not differ between levels of HD, though feeding percentages were larger at the lower HD site. This indicates that males in the present study devoted equivalent amounts of time to food acquisition, despite the difference in fruit availability between sites. It is possible that the higher HD male was able to maintain feeding percentages similar to those of the lower HD male by feeding more often on insects, which were previously shown to comprise a large percentage (44%) of *P. oenanthe* diet (DeLuycker 2007, 2012). Since I did not systematically record which resources study subjects consumed, I was unable to further investigate this possibility. Prior research has indicated that

fruit is a major component of the diet of *P. oenanthe* (40%) (DeLuycker 2007), however the results in the present study suggest that fruit is less important to *P. oenanthe* than previously thought.

Alternatively, the male at the higher HD site may have been able to supplement natural foraging with anthropogenic foraging to maintain equivalent feeding levels. According to *post-hoc* χ^2 tests, the male at the higher HD site engaged in anthropogenic foraging significantly more often than the male at the lower HD site. All study group members at both sites entered human-occupied areas to feed on plantains (a high value food) at least once during data collection. Titi monkeys risked confronting humans and dogs during these excursions, though I never witnessed any such encounters. It is unclear whether titi monkeys employed this foraging tactic due to reduced fruit availability, or if anthropogenic resources were preferred to natural ones despite the accompanying risks. Given the elevated percentage of anthropogenic foraging at the higher HD site, it is reasonable to suggest that this strategy was used more often to compensate for the overall lower abundance of fruit. I did not consider human resources in my prior evaluation of fruit availability; however, titi monkeys appeared to have equal access to these foods at both sites.

None of the predictions regarding the influence of season were supported by the results. First, there were no differences in respective percentages of activities in any category between seasons. Second, males fed more often in the dry season, contradicting my expectations of decreased feeding during this period. The influence of seasonality on feeding was non-significant according to fixed effects tests, however the results indicated that it might be somewhat influential on this behavior ($P = 0.0629$). Seasonality has been shown to affect feeding behavior in other studies on titi monkeys. For example, *P. oenanthe* and *C. nigrifrons* fed more often during the wet than in the dry season, in line with a time minimization (DeLuycker 2007; Nagy-Reis and Setz 2017).

In support of my predictions, I found that wider daily temperature ranges were associated with increased resting and a reduction in traveling and feeding. Social activity also occurred non-significantly less frequently as temperature ranges increased, which was in the expected direction. These outcomes provide evidence of behavioral thermoregulation by *P. oenanthe*, which agrees with DeLuycker's (2007) study of this species. My findings are also in line with research on thermal stress in other primates (*Cebus capucinus*: Campos and Fedigan 2009; *Hoolock leuconedys*: Fan *et al.* 2013). Changes in *P. oenanthe* traveling are expected since arboreal locomotion in this small (1.0 kg) species is characterized by movements (for example, hopping, jumping, clambering, leaping, and climbing) (DeLuycker 2007) that are evidently energetically expensive (Hanna and Schmitt 2011) and more so when carrying infants (see, for example, Tardif 1994; Schradin and Anzenberger 2001). Prey foraging in this species involves propelling the body with quick and powerful movements like grabbing and lunging (DeLuycker 2012),

and is made more difficult when carrying and infants. Given these potential costs, titi monkeys likely traveled and fed less under increased thermal stress in order to conserve energy.

Activity percentages varied according to infant age as predicted. Males rested less often and increased traveling and feeding as infants grew older. I expected this result based on prior titi monkey research suggesting that infant care might conflict with important activities, including foraging (Wright 1984; DeLuycker 2007). Though infant transportation does not affect foraging success of fathers *per se*, foraging percentages are lower when males carry infants than when they do not (DeLuycker 2007). It has been suggested that *P. oenanthe* fathers feed less often while transporting infants because this behavior competes with predator vigilance (DeLuycker 2007). Another factor that may explain why carrying impacts foraging is its impact on traveling speeds. For example, captive *S. oedipus* adults moved more slowly when carrying infants for longer durations and as infants grew heavier (Caperos *et al.* 2012; see also Schradin and Anzenberger 2001). If infant carrying hampers the ability of *P. oenanthe* carriers to move quickly, then a strategy of reducing detection by predators through crypticity rather than relying on evasion only could be more successful in the long term. I did not witness any instances of predation, but I observed titi monkeys adopt cryptic behavior when potential predators (including hawks, dogs, and humans) were near.

Though traveling was less common during younger infant ages, it is unclear whether significant costs accompany infant transport for *P. oenanthe* fathers. Sánchez *et al.* (1999) explored the physical costs of paternal carrying in a study on captive cotton-top tamarins. Infant carrying reduced both feeding and traveling time in fathers. Paternal caregivers also lost weight during weeks 0–5 of infant age when they carried infants most frequently and gained weight thereafter as infants traveled independently for a majority of the time. Similarly, another captive study showed that *S. oedipus* fathers lost weight (range 1.3–10.8%) following the birth of infants, and that fathers with no alloparental helpers lost the most weight (10.0–10.8%) (Achenbach and Snowdon 2002). Based on such findings, I would expect that *P. oenanthe* fathers also lose weight when infant carrying durations are longest and regain weight as carrying declines. However, prior research has indicated that carrying costs are lower for titi monkeys compared with smaller Neotropical primates (Tardif 1994). Additional data and conditions should be explored to better understand these changes.

As a final caveat, I acknowledge that data trends (or lack thereof) may be related to the small sample size, especially across seasons. In addition, data collection did not consistently cover all the study groups' waking hours and thus the estimates presented here do not represent a true time budget for *P. oenanthe* males. This is an important consideration when day lengths differ given that time-adjusted budgets reveal greater variation among groups (Ferrari and Hilário 2014). Nevertheless, the findings indicate that males altered

their time allocation patterns to manage a variety of co-occurring energetic challenges.

Overall, the results indicate that habitat destruction, temperature, and infant age had roles in shaping the activity patterns of *P. oenanthe* males. Understanding how anthropogenic activities affect this Critically Endangered species is vital for conservation efforts (Shanee *et al.* 2013), yet few behavioral studies have been conducted on *P. oenanthe* (DeLuycker 2007, 2012, 2014). Primate research has demonstrated that human-caused habitat disturbance alters typical activity patterns and challenges the ability of primates to persist in impacted areas (de Almeida-Rocha *et al.* 2017). I observed such changes in the present study, including anthropogenic foraging by *P. oenanthe*. Based on the results, I suggest that conservation strategies should aim to protect larger areas of forest habitat where *P. oenanthe* behavior is less likely to be disrupted. I also recommend that population management should focus on preventing opportunities for *P. oenanthe* to engage in anthropogenic foraging as this can increase the risk of disease, injury, and death (Tarara *et al.* 1985; Beamish 2009).

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Ethical note

This research complied with the animal use protocol established by the authors' university Institutional Animal Care and Use Committee, followed the IPS Code of Best Practices for Field Primatology, and adhered to all legalities in Peru (Permit #s: N°0208-2012-AG-DGFFS-DGEFFS and N°329-2016-SERFOR-DGGSPFFS).

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