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Abstract

Parenting in mantled howler monkeys (*Alouatta palliata*) requires a new set of energetic and behavioural demands. Because of constraints presented by the infant, as well as the increased energy requirements associated with mothering, parenting females need to change their activity patterns to ensure the successful upbringing of their offspring. This study of wild mantled howler monkeys was conducted to examine differences in activity between parenting and non-parenting adult females. Twenty two hours of continuous sampling on focal individuals was collected over the course of ten days in August at a study site in Nicaragua. It was found that the two groups do differ in their activity patterns: parenting females spent a larger percent of their time resting, feeding and interacting, but a lower percent of their time travelling when compared to non-parenting females. Further, it was found that parenting females engaged in scanning behaviours more frequently, and engaged in bridging (a locomotor behaviour) less frequently. These results suggest that parenting female mantled howler monkeys adopt an energy-minimizing activity pattern wherein the mothers compensate for their increased energetic requirements by only slightly increasing their food intake and instead drastically increasing the amount of time spent resting.

Keywords

activity budgets, resting, feeding, behaviour, ecology, infant, mother-infant, social interaction, vigilance, locomotion

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Behavioural Changes in Parenting Female Mantled Howler Monkeys (*Alouatta palliata*)

Emma Cancelliere

Introduction

As with all primates, female mantled howler monkeys (*Alouatta palliata*) invest heavily in their offspring. Mantled howler monkey infants may remain with their mothers for upwards of three years, and will suckle for up to 22 months (Ballcells and Baro 2009). This prolonged period of infant dependency is not without cost to the mother. The energetic costs of carrying a fetus to term, and subsequently lactating for a prolonged period, are high (Ballcells and Baro 2009; Milton, Casey, and Casey 1979). To compensate for these new requirements, and to adjust to the continual presence of a vulnerable infant, female mantled howler monkeys must alter their behavioural repertoire or face difficulties in maintaining their own, and their infant's, health.

In order to test whether the increased energetic requirements of parenting mantled howler monkeys affect behaviour, I undertook a study of the behaviour of both parenting and non-parenting females. Differences observed in feeding behaviour, resting behaviour, or locomotion may represent the behavioural strategies used by parenting mantled howler monkeys to compensate for increased energetic requirements.

Pregnancy and lactation are highly energetically demanding tasks. Periods of food shortage and nutritional stress are more detrimental to lactating female howler monkeys than to any other category of individual (Milton, Casey, and Casey 1979). This increased nutritional demand should cause parenting females to feed more frequently than non-parenting females. Further, given the unique difficulties

presented by the mantled howler monkey's folivorous diet, increased feeding time may necessitate a larger proportion of time dedicated to resting. This resting is needed for the body to digest the relatively indigestible leaf material that typifies the mantled howler monkey's diet (Milton 1980).

Nutritional requirements aside, parenting presents new challenges in terms of infant care and responsibility. The socialization of mantled howler monkey infants is critical to their survival and future reproductive success (Clarke 1990). In order to engage an infant socially and ensure their integration into their natal group, a parenting female may engage in social behaviour more frequently than non-parenting group members (Ballcells and Baro 2009).

The vulnerability of young offspring places them at much higher risk of conspecific attacks (Treves, Drescher, and Snowdon 2003). In order to compensate for these risks, parents should increase their vigilance around their infants (Treves, Drescher, and Ingrisano 2001). This effect has been noted in black howler monkeys (*Alouatta pigra*), in which parenting females become more vigilant when their offspring are conspicuous and therefore, most vulnerable to attack (Treves, Drescher, and Snowdon 2003). These behaviours should also be found in mantled howler monkeys and parenting females should therefore be more vigilant than non-parenting females. Additionally, the risk to young offspring increases with distance from its mother (Arroyo-Rodriguez et al. 2007). Parenting females should likely stay within a certain range of their offspring, both for socialization and to ensure that they are not in any immediate danger (Arroyo-Rodriguez et al. 2007; Treves, Drescher, and Snowdon 2003). Generally, the maximum distance between mother and offspring is found to be between five to ten meters depending on

Class	Definition
Parenting Females	Adult females who interacted with and/or had an infant cling to them for at least one minute prior to the beginning of a focal sample, and remained within 10 meters of said infant for the entire duration of the focal sample.
Non-Parenting Females	Adult females who had no infant cling to them at any point during the focal sample.

Table 1: Classes of individual studied.

infant age, behaviours at the time, and nearest neighbours (Arroyo-Rodriguez et al. 2007; Ballcells and Baro, 2009). Parenting females should demonstrate a lessened degree of mobility given that they are constrained by the location of their infants (Arroyo-Rodriguez et al. 2007).

The need for mother-infant proximity creates limitations in type of movement for parenting females, as well. Infants often lack the balance and skill needed to manoeuvre through a difficult arboreal habitat (Ballcells and Baro 2009). As a result, successful parents must account for their infant's capabilities in planning their own movement. Carrying an infant across distances is energetically expensive and risky, motivating mothering mantled howler monkeys to minimize the amount of time spent locomoting. The reduction in locomotion may also extend to crossing between tree gaps. Bridging locomotor behaviours are risky for an uncoordinated infant, and thus should be reduced in parenting females to avoid unnecessary risk.

When presented with the new suite of energetic and behavioural demands that accompany becoming a mother, a female's activity pattern has to change accordingly to maximize both her own and her infant's health and fitness. This study on female mantled howler monkeys, both parenting and non-parenting, acts as an attempt to assess what, if any, behavioural changes are made to accommodate the challenges of parenting.

Methods

This study was conducted on the

island of Ometepe, a 254km² area within Lake Nicaragua, in Nicaragua. The study subjects are a group of mantled howler monkeys who inhabit a dry tropical forest fragment of approximately 30 hectares, of which 12.7 hectares were used in data collection. Data collection occurred over a ten day period from August 2nd to August 12th, 2010. Two to five hours of data were collected per day and samples were taken between the hours of 06:00 and 16:00, with the majority of samples taken between 07:00 and 14:00.

At least two distinct groups of mantled howler monkey live in the study area, and data were collected from both groups. Individuals were identified on a daily basis using distinguishing characteristics including pelage colour, facial features, overall body size, mantle colour and length, and unusual markings or deformities. To prevent oversampling, each individual was only sampled once per day, when identity could be ascertained. No order or priority was given to classes of individual in terms of choosing a subject for observational samples of focal individuals.

For the purposes of the study, two classes of individual were identified: parenting females and non-parenting females (Table 1). In instances where an infant strayed farther than ten meters from a female identified as a parent for more than two minutes, the observation was aborted because maternity could not be confirmed.

Data were collected via 30 minutes of continuous observational follows of focal individuals, during which the following behavioural states were recorded: feeding,

Behaviour	Definition
Feeding (state)	To put food in mouth, either directly or first manipulating it in some way, and/or swallowing it.
Resting (state)	Any behaviour in which no locomotion occurs and at least 50% of the body is on substrate for a minimum of ten seconds.
Interacting (state)	Any behaviour (including play, groom and nurse) in which two individuals are clearly in physical contact and active (not resting) for at least three seconds.
Travelling (state)	Any locomotor behaviours further than one meter in any direction.
Scanning (event)	Head is upright or lifted, and turns or swivels at least once in any direction with eyes open for at least two seconds.
Bridging (event)	Any locomotor behaviour that carries an individual from one tree to another.

Table 2: Recorded behaviours (both states and events)

	Rate of Scanning	Rate of Bridging
Parenting Females	0.7	0.1
Non-parenting Females	0.4	0.2

Table 3: Rates of behavioural events (per minute).

resting, interacting and travelling (Table 2). Within each behavioural state, the frequency of two events, scanning and bridging, were recorded whenever they occurred (Table 3). Any samples which ended prior to the 20 minute mark were immediately aborted. If a focal individual was out of sight for two consecutive minutes or for ten minutes of the total sample, the sample was also aborted.

Data were analyzed using comparative statistics of parenting against non-parenting females. Averages were calculated for each behavioural state by using the total

duration of each behaviour for each group of females. For scanning and bridging events, the rate per minute was calculated.

Results

In total, 44 focal samples were collected; 21 were of parenting females and 23 of non-parenting females. This amounted to a total of 617 minutes and 28 seconds of data for parenting females and 669 minutes and 19 seconds for non-parenting females. Time spent in each behavioural state was tallied for each class of individual and converted into a percentage of total time spent in each state. The frequency of behavioural events per sample was tallied and divided by the length of the sample to obtain a *per minute* rate of the event occurring.

There were clear differences in the activity budgets of parenting versus non-parenting females (Figure 1). Parenting females rested 83.0% of their time, fed 7.9% of their time, traveled 7.1% of their time,

and interacted 2.0% of their time. Non-parenting females spent 69.6% of their time resting, 4.5% feeding, 25.6% travelling, and 0.3% interacting.

Parenting and non-parenting females also exhibited variation in frequency of scanning and bridging behaviours. There were marked differences in the rate per minute that each behavioural event occurred during the sample period. Parenting females scanned more frequently, and bridged less often, than non-parenting females (Table 3).

Discussion

It is well established in previous literature that the energetic requirements and behavioural repertoire of parenting females in all primate species differ from those of non-parenting females (Milton 1980; Milton, Casey, and Casey 1979; Treves, Drescher, and Snowdon 2003). The results of

this study are consistent with these findings.

Parenting females spend a larger amount of time resting than non-parenting females. This difference is related to the increased nutritional requirements of parenting females in two manners. Firstly, by resting more and moving less, parenting females are conserving energy and reducing their energetic requirements. Due to the difficulty in digesting fibrous folivorous materials, increased feeding necessitates longer periods of rest for digestion to occur (Milton 1980). Secondly, the increase in time spent resting could be related to the parenting female needing to watch her infant (Treves, Drescher, and Snowdon 2003). A resting mother can be more vigilant and may be able to react more quickly in the event of a traumatic incident (Arroyo-Rodriguez et al. 2007). Without the constraint of a dependent infant or the energetic burden of

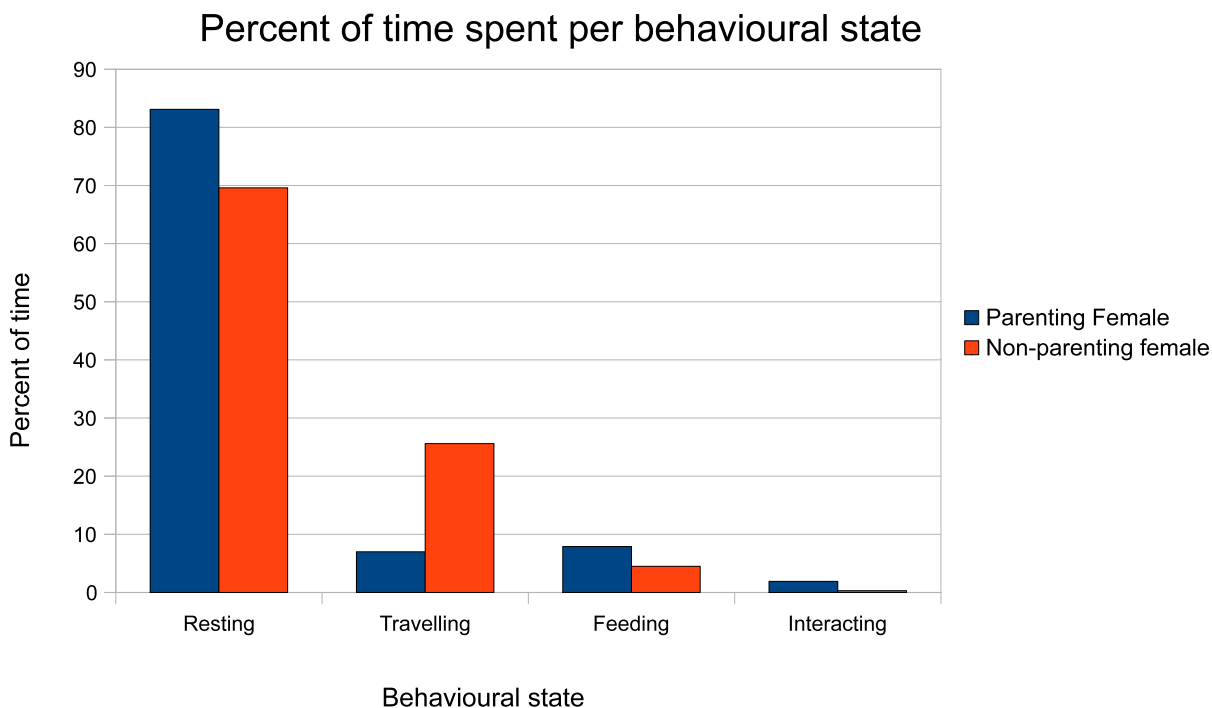


Figure 1: Average total times spent per behaviour, parenting and non-parenting females.

lactation/ recuperation, non-parenting females are able to rest less and dedicate more time to travel both within and between trees.

The security of the infant seems to be an underlying cause to many of the observed differences between parenting and non-parenting females. Treves and colleagues (2003) noted that female black howler monkeys (*Alouatta pigra*) with infants and juveniles were more vigilant than non-parenting females. I found this to also be the case in the studied group of mantled howler monkeys, as parenting females scanned the area around themselves and their infants more often than non-parenting females scanned the immediate area around themselves.

Non-parenting females were less inclined to scan and engage in vigilance behaviours because of their lack of offspring to protect, and because of the presence of males in their immediate surroundings. Male members of the genus *Alouatta* will often take the role of sentinel while females feed and rest (Milton 1980). In groups of black howler monkeys with no infants, males spend more time being vigilant than their female counterparts (Treves, Drescher, and Ingrisano 2001). Similarly, I found that non-parenting females engaged in vigilant behaviour at a low rate. The relationship between context and vigilance is clearly complex, and would make an interesting subject for future study.

Pregnant and lactating female mantled howler monkeys have drastically different nutritional requirements. Their increased energetic needs necessitate a larger portion of time dedicated to feeding and foraging (Milton 1980). Further, it has been suggested that feeding and foraging serve a teaching role by demonstrating these behaviours to infants (Arroyo-Rodriguez et al. 2007). These reasons could explain why feeding behaviours were observed more

frequently in parenting females than in non-parenting females. However, the results may not fully reflect the extent of a parenting female's high energetic requirements. Although this study shows that parenting females spend on average 3.4% more time feeding than non-parenting females, the energetic requirements of a pregnant or lactating female ranges from 25-50% greater than that of a normal adult female mantled howler monkeys. This discrepancy could be explained by the large increase in time parenting females spent resting. As energy minimizers, parenting females could be attempting to reconcile their new energy expenditures by resting to conserve energy rather than feeding more, as foraging and feeding is energetically expensive. Additionally, feeding behaviours imply less attention being paid to the infant, a finding noted by Treves and colleagues (2003) in black howler monkeys. For this reason, minimizing expended energy may be a more effective manner of meeting metabolic requirements than increasing intake.

Consistent with this energy-minimizing strategy, parenting females spend a significantly lower percent of their activity budget engaged in locomotor behaviours. Much of the time that would otherwise be spent traveling is being re-allocated to resting in parenting females. This could also be a protective mechanism to lower the risk of infant vulnerability. An infant who is resting and clinging to a mother is at a lower risk of predation or conspecific attack than a conspicuous, moving infant (Treves, Drescher, and Snowdon 2003). Reduced mobility may also prevent the accidental deaths of uncoordinated infants who are unable to navigate unstable environments independently. The latter point is very connected to the rate of bridging by parenting females. All locomotion in the early stages of parenting occurs when the infant is securely clinging

to the mother, to minimize the risk of infant death (Arroyo-Rodríguez et al. 2007). This creates an extra burden for the mother, who must account for the infant's weight and posture when balancing and moving. Bridging, which often involves leaping or swinging, can thus be viewed as a high-risk locomotor activity. Without having to ensure that a less-coordinated infant is also able to bridge the same tree, non-parenting females are freer to travel between and throughout trees.

The results of this study indicate that parenting and non-parenting female mantled howler monkeys do allocate their time in different ways. The proportion of time dedicated to daily activities differs between the two groups, potentially as a product of differing energetic demands. The increase in time spent resting and decrease in locomotion indicates that mantled howler monkeys shift their behaviour in order to minimize expended energy. By minimizing expended energy, parenting female mantled howler monkeys are able to compensate for the increased energetic demands associated with motherhood. This energy minimizing is accompanied by behavioural changes which may further increase their infants chances at survival, such as increased vigilance or decreased *risky* movement (bridging). The findings of this study corroborate with similar studies on parental investment, supporting the belief that primate mothers alter their behaviour to ensure the survival of their high-investment infants. The extent to which a mother changes her behaviours to accommodate a dependent infant is variable across both individuals, groups and species, and is a field of study which merits future investigation to further our understandings.

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