RESEARCH ARTICLE

WILEY | AMERICAN JOURNAL OF PRIMATOLOGY

Energetic constraints on the reproduction of female mantled howlers

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Funding information
Consejo Nacional de Ciencia y Tecnología, Grant number: 254217

The reproductive process of female primates is energetically constrained. However, while there is extensive evidence about factors that influence the maintenance of gestation and lactation, less is known about energetic correlates of cycling and the occurrence of conception in wild primates. We examined how female physical condition affected the occurrence of conception and interbirth intervals (IBI) in female mantled howler monkeys, a species in which females experience long non-conceptive periods. For 6 years we followed 7 females at La Flor de Catemaco (Los Tuxtlas, Mexico). In addition to noting the presence of dependent immatures, we collected fecal samples that were analyzed for thyroid hormone and glucocorticoid metabolite concentrations ($N = 1,460$). Conception was more likely following months when females were not lactating and had higher thyroid hormone and lower glucocorticoid levels. IBIs were shorter when females had higher thyroid hormone and lower glucocorticoid levels, and when the infant at the beginning of the interval died. Due to their obvious impact on female fecundity and fertility, gestation and lactation are the stages of the reproductive process that have traditionally received more attention in studies of female reproductive performance. Still, the cycling stage accounts for a large proportion of IBIs in many primate species. Here we demonstrate that the reproductive rates of female mantled howler monkeys are energetically constrained: both the occurrence of conception and IBI are positively affected by female energetic condition.

KEYWORDS
Alouatta, conception, glucocorticoids, interbirth interval, reproductive ecology, thyroid hormones

1 | INTRODUCTION

The reproduction of female primates is energetically constrained: gestation, lactation, and ovulation may be suppressed when females do not meet their energy requirements (e.g., Dufour & Sauther, 2002; Ellison, 2003; Fürtbauer, Heistermann, Schülke, & Ostner, 2013; McCabe & Emery Thompson, 2013). Although alloparenting has been documented in several species (e.g., Chism, 2000; Ross & MacLarnon, 2000), mothers are consistently the main providers of parental investment (192 of 230

species listed in Opie, Atkinson, Dunbar, and Shultz (2013)). Therefore, studying how females allocate energy throughout the reproductive process is critical to understand the evolution of their reproductive strategies and to predict variation in fitness.

Gestation and lactation are the most expensive stages of the female reproductive process, as they may entail 25 and 25–100% increases in energetic requirements, respectively (Altmann & Samuels, 1992; Key & Ross, 1999; Portman, 1970; Roberts, Cole, & Coward, 1985; van Noordwijk, Kuzawa, & van Schaik, 2013). In some primate

species, however, variation in their duration may be smaller than variation in time spent cycling before conceiving. For example, in mandrills (*Mandrillus sphinx*) gestation ranges between 168 and 183 days (a 9% difference), lactational or postpartum amenorrhea ranges between 74 and 538 days (151% difference), and cycling ranges between 24 and 192 days (163% difference; Setchell, Lee, Wickings, & Dixson, 2002; Setchell & Wickings, 2004). Thus, factors affecting the occurrence of conception may be highly influential in female reproductive rates.

The occurrence of conception is influenced by social (e.g., Beehner & Lu, 2013) and ecological factors (e.g., Emery Thompson, 2013). Overall, this evidence suggests that female reproductive function depends on energy balance, and recent studies are starting to disclose the mechanisms underlying conception probabilities in female primates. Specifically, a positive energy balance has been linked to the occurrence of conception in female chimpanzees (*Pan troglodytes*: Emery Thompson, Muller, & Wrangham, 2012) and Sanje mangabeys (*Cercocebus sanjei*: McCabe & Emery Thompson, 2013), as well as in women (reviewed in Ellison (2003)). Positive balance is associated with higher insulin levels, which in turn facilitate steroidogenesis, and as a consequence normal ovarian function (Greisen, Ledet, & Ovesen, 2001; Willis, Mason, Gilling-Smith, & Franks, 1996). Despite such progress, to understand the reproductive function of female primates from a comparative perspective we need data on the association between energy balance and conception occurrence from more species.

In recent years, the non-invasive monitoring of thyroid and glucocorticoid hormones has allowed exploring the energetics of wildlife (e.g., Emery Thompson, 2016). Both hormone families are involved in metabolic processes, including gluconeogenesis in individuals facing energetic challenges (Kim, 2008; Sapolsky, Romero, & Munck, 2000). However, whereas glucocorticoid secretion occurs in response to environmental (e.g., food availability: 2012; Bourbonnais, Nelson, Cattet, Darimont, & Stenhouse, 2013), physical (e.g., climate: Houser, Yeates, & Crocker, 2011), intrinsic (e.g., reproductive status: Viblac, Gineste, Robin, & Groscolas, 2016), and psychological (e.g., social stress: Stocker, Munteanu, Stoewe, Schwab, Palme, & Bugnyar, 2016) demands, thyroid hormones seem to be unaffected by psychological stress (Gobush, Booth, & Wasser, 2014). Therefore, these hormones provide complementary information on the physiological mechanisms associated with coping with energetic demands. In this context, their measurement may assist in assessing the relationship between energy balance and reproduction.

Howler monkeys (*Alouatta* spp.) are a genus of at least 12 species (Cortés-Ortiz, Rylands, & Mittermeier, 2015) of diurnal, arboreal, frugivorous-folivorous Neotropical primates that distribute from Mexico to Argentina. Compared to other atelines (i.e., *Ateles*, *Brachyteles*, and *Lagothrix*), howler monkeys begin reproducing at an early age and interbirth intervals (IBI) are shorter (Di Fiore et al., 2011). However, female mantled howler monkeys (*A. palliata*) have the longest reported cycling period among atelines, a maximum of 15 months to conception (Di Fiore et al., 2011). Given a mean IBI of 22.5 months in this species (range = 18–25 months), the mean cycling period (12.8 months; range = 11–24 months) accounts for 56.9% of the IBI, compared with 27.6% for gestation (mean = 6.2, range = 6–6.5 months), and 15.6% for lactational amenorrhea (mean = 3.5 months, range = 3–4 months; Glander, 1980). This partitioning of time among the different stages of the reproductive process suggests that conception may be particularly constrained in this species.

Recently, our team demonstrated that compared with gestating and lactating females, cycling mantled howler monkey females have lower energetic condition, as attested by lower urinary C-peptide and fecal thyroid hormone levels (Cano-Huertes et al., 2017; Dias, Coyohua-Fuentes, Canales-Espinosa, Chavira Ramírez, & Rangel-Negrín, 2017). Furthermore, only in cycling females was energetic condition positively related with food availability (Cano-Huertes et al., 2017), suggesting that conception probabilities are constrained by access to nutrients or energy. Given this evidence, and that the cycling stage accounts for the largest proportion of IBI, it could be expected that female reproductive rates are influenced by female energetic condition during the cycling stage. To examine this hypothesis, we tested two predictions. First, we predicted that conception probabilities should be positively related with female energetic condition. To test this prediction, we used four predictors. Two were fecal metabolites of hormones related to energy allocation in vertebrates (triiodothyronine—thyroid hormone for simplicity—and glucocorticoids: Dias et al., 2017). The third was the occurrence of lactation, which negatively affects female energetic condition in mammals (e.g., Gittleman & Thompson, 1988; Valeggia & Ellison, 2004). The fourth was lactation stage, as maternal condition varies through lactation (e.g., Emery Thompson et al., 2012). In *A. palliata*, maternal physical condition is the lowest at early and late lactation, compared with mid lactation (Dias, Cano-Huertes, Coyohua-Fuentes, Chavira-Ramírez, Canales-Espinosa & Rangel-Negrín, 2018). Therefore, we expected that conception occurred when females were not lactating, and if they were lactating, were in mid lactation, had high thyroid hormone levels, a demonstrated proxy for energy acquisition in this species (Dias et al., 2017; Wasser et al., 2010), and had low glucocorticoid levels. Although glucocorticoids can respond to a variety of different ecological and social challenges, prior examinations of our population suggest that they are a proxy for energy expenditure in this species (Dias et al., 2017; Dunn, Cristóbal-Azkarate, Schulte-Herbrüggen, Chavira, & Veà, 2013). Second, we predicted that the duration of IBI should be negatively related with female energetic condition. Accordingly, we expected longer IBI when females had lower thyroid hormone and higher glucocorticoid levels (i.e., were presumed to be in a negative energy balance). Due to the negative effects of lactation on female energetic condition, we also expected shorter IBI when infants at the beginning of the IBI died (i.e., when females were relieved from the energetic burden of lactation).

2 | METHODS

2.1 | Ethical note

Our study was noninvasive and adhered to the American Society of Primatologists Principles for the Ethical Treatment of Non-Human

Primates. Research protocols were approved by the Secretaria de Medio Ambiente y Recursos Naturales (permits SGPA/DGVS/10637/11 and SGPA/DGVS/04999/14) and adhered to the legal requirements of Mexican law (NOM-059-SEMARNAT-2010).

2.2 | Study site and subjects

The study was conducted from January 2012 to December 2017 at La Flor de Catemaco (Los Tuxtlas, Mexico; 18°26′39″ N, 95°02′57″ W). A total of 22 mantled howler monkeys live in this ca. 100-ha evergreen forest (Dias et al., 2017, 2018). At the onset of the study, three females had infants, whose ages were estimated on the basis of morphology and behavior (Balcells & Veà, 2009). During the study, we recorded another 18 births. Overall, births were scattered throughout the year (Figure 1). We studied seven adult females belonging to two groups (Table 1). Each month we sampled each group for a mean (±SD) of 10 ± 3 days and classified females in one of three reproductive states: lactating (i.e., females with an associated immature of 0–20 months: Balcells and Veà (2009)); gestating (i.e., females in the period encompassing the day before parturition to 186 days back from that date, which corresponds to the duration of pregnancy in this species: SD = 6 days, Glander (1980)); or cycling (neither lactating nor gestating). Lactating females were further classified in lactation categories according to the age of their immatures: early lactation, when immatures were 0 to <4 months; mid lactation, when immatures were 4–<15 months; late lactation, when immatures were 15–20 months (Dias et al., 2018). The occurrence of conception was inferred by counting back 186 days from birth dates. We based this classification on observations of newborns and immature presence during visits to the study groups. If in a particular month a female was recorded in more than one reproductive state, we classified her in the category for which she had more recordings.

2.3 | Fecal sample collection and hormone assays

We collected fecal samples from females immediately after deposition whenever they were unequivocally matched to subject identity and were uncontaminated by urine. We deposited samples in polyethylene bags labeled with the date and identity of each individual. We kept samples in a cooler with frozen gel packs while in the field and stored them at the end of the day in a freezer at −20 °C until processing. We extracted fecal triiodothyronine and glucocorticoid metabolites following Wasser et al. (2000). We measured thyroid hormone in fecal samples with a chemiluminescent enzyme immunoassay commercial kit (Total T3 Immulite, Siemens Healthcare Diagnostics Products Ltd., Llanberis, UK; sensitivity = 0.59 nmol/L; calibration range = 0.61–9.2 nmol/L) and an Immulite 1000 analyzer (Siemens). We determined glucocorticoid levels in feces via radioimmunoassay (Izotop, Institute of Isotopes Ltd., Budapest, Hungary; sensitivity = 2.9 nmol/L; calibration range = 0–1600 nmol/L) and a gamma counter (Cobra Model E5005, Packard, Inc., Downers Grove, IL). Protocols that we used to extract and quantify thyroid hormone and glucocorticoid levels in feces have been previously validated to detect thyroid function and the activation of the HPA axis, respectively, in mantled howler monkeys (Dias et al., 2017; Gómez-Espinosa, Rangel-Negrín, Chavira, Canales-Espinosa, & Dias, 2014). Analytical validation of our assays is reported in Table S1. All samples were run in duplicate and we report hormone levels as ng/g of dry feces. We analyzed five fecal samples per female per sampling month (excluding gestation months), in a total of 1,460 samples.
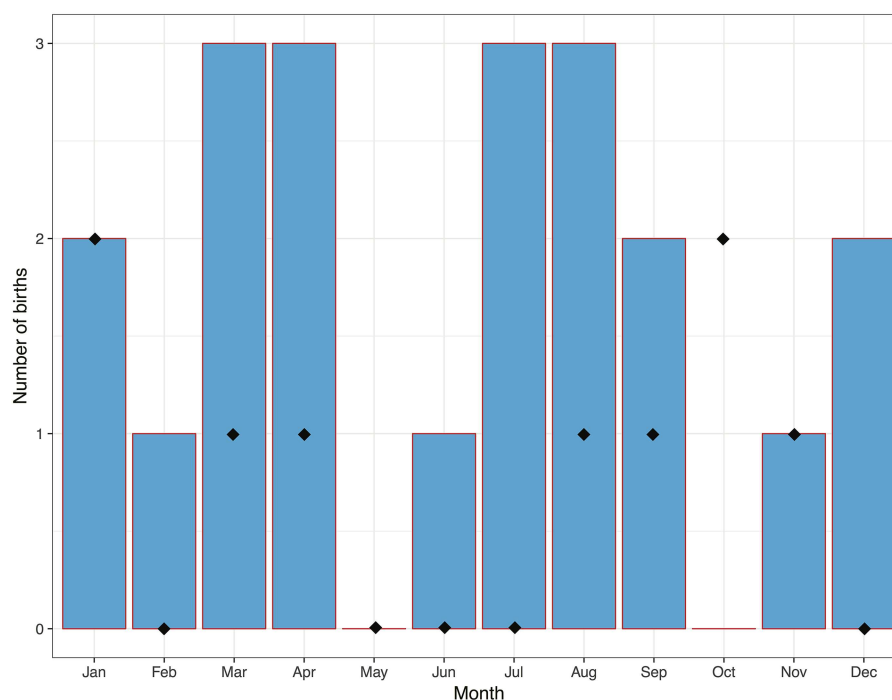
FIGURE 1 The number of births per month (blue bars) for seven adult female mantled howler monkeys studied between 2012 and 2017 in La Flor de Catemaco (Los Tuxtlas, Mexico). Infant deaths represented as black diamonds

TABLE 1 Reproductive data collected for female mantled howler monkeys studied between January 2012 and December 2017

Female[a]	Number of births	% of infants that survived	Sampling months	Fecal samples analyzed
H1[b]	4	100	72	305
H2	2	0	25	75
HA	3	100	55	190
HB[c]	1	0	15	40
HCC[b]	3	66.7	72	310
HN[b]	3	100	72	310
HPM	5	40	72	230
Means ± SD	2.8 ± 1.3	51.1 ± 45.5	54.7 ± 24.7	208.6 ± 113.2

[a]Female H2 died in December 2013. Females HA and HB were included in the study in June 2013 and October 2016, respectively, when they started copulating with males. Before they were classified as subadults.
[b]This female had an infant at the beginning of the study, for which age was estimated on the basis of morphology and behavior.
[c]An IBI could not be calculated for this female, as after the death of her first infant, she did not give birth to a new infant before the end of the study.

2.4 | Data analysis

We calculated IBI as the number of days encompassed between two consecutive births. To test our first prediction, that conception is influenced by short-term variation in female energetic condition, we ran a binomial generalized linear mixed model (GLMM) (with logit link-function) using the occurrence of lactation (quantified as a yes/no dichotomy), lactation stage (i.e., non-lactating, in early, mid, or late lactation), mean thyroid hormone levels, and mean glucocorticoid levels per female per month as fixed predictors for the occurrence of conception in the next month (quantified as a yes/no dichotomy). For this prediction, we used 292 female-months. To account for the repeated sampling of each female in different months, we included female identity as a random factor in this analysis. Thyroid hormone and glucocorticoid levels were not collinear (variance inflation factor = 2.5; function "corvif": Zuur, Ieno, Walker, Saveliev and Smith (2009)), and were only weakly correlated ($r = −0.16$, $p = 0.045$).

To test our second hypothesis, that IBI is influenced by long-term variation in female energetic condition, we ran a Poisson GLMM (with log link-function) using the survival of the infant at the beginning of the interval, mean thyroid hormone levels, and mean glucocorticoid levels per female per IBI as fixed predictors of IBI (quantified in days). We used the 14 complete IBI that we recorded during the study. We included female identity as a random factor in this analysis. Again, thyroid hormone and glucocorticoid levels were not collinear (variance inflation factor = 1.4) and were weakly correlated ($r = −0.36$, $p = 0.031$).

Before running models, we standardized numerical variables as they were on very different scales of magnitude using function "stdize" in R package "MuMln" (Barton, 2018). We verified the underlying assumptions of the models visually with Q-Q plots of residuals fitted against predicted values. We used R package "lme4" (Bates, Maechler, Bolker, & Walker, 2018) with function "glmer" to obtain GLMM parameters, and function "confint" to obtain confidence intervals for fixed factors using package "stats" (R Core Team, 2018). To ascertain whether our complete models, including fixed and random predictive variables, were a better fit for dependent variables than models including only random factors, we used a likelihood ratio test using function "anova" in R package "stats" (R Core Team, 2018).

3 | RESULTS

Mean ± SE IBI was 669.4 ± 97.3 days (range = 219–1,506 days, $N = 14$; Figure 2). When considering only IBIs in which the infant at the beginning of the IBI survived ($N = 10$), IBI increased to 805.7 ± 90.3 days (range = 492–1,506 days), whereas IBI when infants died ($N = 4$) was 328.5 ± 125.8 days (range = 219–470 days).

3.1 | Conception probabilities

The complete model to explain variation in conception probabilities in female mantled howler monkeys was significantly different from the null model (likelihood ratio test: $\chi^2_4 = 25.2$, $p < 0.001$). Conception
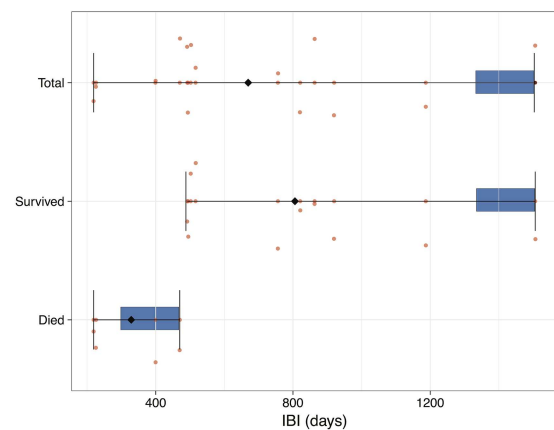
FIGURE 2 Interbirth intervals of female mantled howler monkeys. Total IBI, IBI when the infant at the beginning of the interval survived, and when the infant died are represented. Black diamonds are the means, whiskers are the ranges, and red dots are the individual IBI. For reference, the duration of gestation (186 days) was imposed to the maximum IBI as blue rectangles

probabilities in a given month were affected by the occurrence of lactation, thyroid hormone levels, and glucocorticoid levels in the previous month, but were not affect by infant age in females that were lactating (Table 2). Conception probabilities varied from 1.5 to 13.1% between months when females were and were not lactating in the previous month, respectively. Additionally, there was a two-fold increase [from (mean ± SE) 298.3 ± 40.2 ng/g to 583.6 ± 2.4 ng/g] and a ten-fold decrease [from (mean ± SE) 495.8 ± 17.2 ng/g to 50.1 ± 15.2 ng/g] in thyroid hormone and glucocorticoid levels, respectively, between months that precede and months that did not precede conceptions (Figure 3a and 3b).

3.2 | Interbirth interval (IBI)

The complete model to explain variation in IBI was significantly different from the null model (likelihood ratio test: $\chi_3^2 = 10.5$, $p < 0.001$). IBIs were affected by the survival of the infant at the beginning of the interval and by both thyroid and glucocorticoid levels of females (Table 3). There was a three-fold decrease in IBI when the infant died at the beginning of the IBI [from (mean ± SE) 337.7 ± 106.8 days to 125.8 ± 62.9 days; Figure 4a)]. Furthermore, IBIs were significantly longer when females had lower thyroid hormone and higher glucocorticoid levels (Figures 4b and 4c).

4 | DISCUSSION

Our results indicate that the reproductive rates of female mantled howler monkeys are influenced by female energetic condition, in the short and in the long-term. In the short-term, conception was more likely following months when females had higher thyroid hormone and lower glucocorticoid levels, and when they were not lactating. Conception probabilities were not related with lactational stage. In the long-term, IBIs were shorter when females had higher thyroid hormone and lower glucocorticoid levels, and when the infant died at the beginning of the IBI.

Howler monkeys have lower birth seasonality than other similar sized New World primates (Di Bitetti & Janson, 2000). Births tend to occur throughout the year (Di Bitetti & Janson, 2000) and in ursine howler monkeys (A. arctoidea) infants that are born outside seasonal birth peaks have survival rates similar to those born during peaks (Crockett & Rudran, 1987). This has been interpreted as a consequence

of their ability to exploit seasonal foods, such as young leaves and unripe fruits (Crockett & Rudran, 1987; Milton, 1982). Birth data from La Flor de Catemaco converges with this evidence, as with the exceptions of May and October, we observed births in all months and infant deaths were scattered through the year. The fact that no infants died during weaning converges with previous suggestions (Cano-Huertes et al., 2017) that this species follows an income-II breeding strategy (Janson & Verdolin, 2005). Income-II breeders schedule reproductive stages to minimize energetic stress for the mothers, instead of reducing energetic stress for immatures, and at La Flor de Catemaco maternal physical condition is positively correlated with food availability and is also higher at mid lactation than in other moments (Dias et al., 2018).

Considering that in this species weaning occurs at around 20 months of age, an early death of infants could result in a considerable shortening of the IBI. Accordingly, all infants that died (N = 7) were <3 months of age, infant survival was an influential factor in IBI length, and IBI was 40% longer when infants survived than when they did not. Hence, our results confirm that female mantled howler monkeys may resume sexual activity shortly after the death of their infants (Glander, 1980). For a 328-day IBI, the loss of a 1-month infant (71.4% of infant deaths occurred at this age) implied a 3-month lag until conception, and for both mean IBI and IBI when infants at the beginning of the interval survived, that lag was even longer. This means that the reproductive performance of females living at La Flor de Catemaco is characterized by long periods of non-conceptive cycling, as described for other populations of this species (e.g., Glander, 1980; Milton, 1982), although we cannot reject unsuccessful implantations or abortions caused by low energetic condition (Garcia-Garcia, 2012; Lujan, Krzemien, Reid, & Van Vugt, 2006; Tardif, Power, Layne, Smucny, & Ziegler, 2004) as alternative causes for prolonged IBI.

Our results support our previous findings that female mantled howler monkeys face energetic constraints to their reproduction (Cano-Huertes et al., 2017). The influence of thyroid hormone levels on the occurrence of conception and reproductive rates is probably associated with both its positive correlation with food intake and its role in regulating energy expenditure/saving strategies (Fisher, 1996; Flier, Harris, & Hollenberg, 2000; Moon, Owens, & MacKenzie, 1999). Glucocorticoids, however, increase under nutritional deficits to mobilize energy reserves (Sapolsky et al., 2000), and have direct inhibitory influences on female reproductive physiology (Moberg, 1991). It is therefore possible that, although lactational amenorrhea suppresses ovarian function for only 3–4 months (Glander, 1980),

TABLE 2 Generalized linear mixed model for variation in conception probabilities in female mantled howler monkeys

Variable	Estimate	SEM	95%CI	Z	p
Intercept	1.49	0.69	0.14–2.86	2.16	0.031
Occurrence of lactation	−3.39	1.38	−6.08–(−0.69)	2.46	0.013
Thyroid hormone	2.51	0.43	0.76–2.45	3.91	<0.001
Glucocorticoids	−1.78	0.02	−1.98–(−0.19)	3.21	0.001
Infant age	0.07	0.09	−0.14–0.24	0.81	0.421
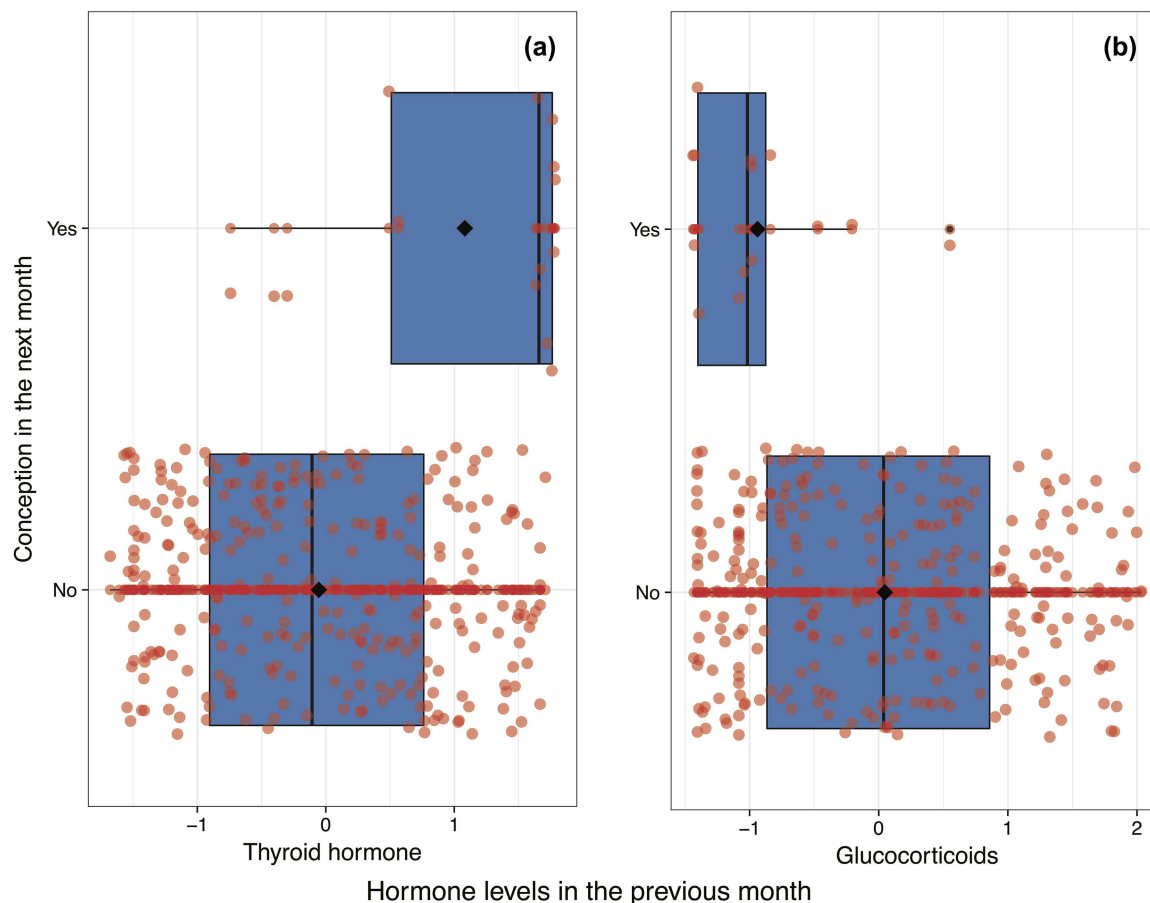
FIGURE 3 The occurrence of conception as a function of thyroid hormone (a) and glucocorticoid (b) levels in the previous month in seven adult female mantled howler monkeys studied between 2012 and 2017 in La Flor de Catemaco (Los Tuxtlas, Mexico). $N = 292$ female/ months. Center lines show the medians, black diamonds are the means, box limits indicate the 25th and 75th percentiles, whiskers extend 1.5 times the interquartile range from the 25th and 75th percentiles, and red dots are data points

ovarian hormone levels remain energetically constrained until weaning, precluding successful conception. This is supported by the fact that, although mid lactation is a less energetically stressful stage than early and late lactation (Dias et al., 2018), the occurrence of conception was not linked to lactation stage. Given that in principle all females have equal access to food resources (i.e., there is no clear priority of access to food resources by some females: Jones (1980)), the lower physical condition of cycling females compared to other females (Cano-Huertes et al., 2017), and of mothers of immatures approaching weaning age than those in mid lactation (Dias et al., 2018), may result from the depletion of maternal energetic condition (i.e., higher glucocorticoid levels) caused by accumulative energetic costs of maternal care (Emery Thompson et al., 2012). This is further supported

by the observation that mothers of infants that survived had IBI that were 6 months in excess of weaning age. It is therefore possible that females require an extended period of positive energy balance to conceive and sustain a successful gestation (Emery Thompson et al., 2012). This may explain why when food availability is high cycling females spend more time feeding and less time resting than females in other reproductive states (Cano-Huertes et al., 2017).

The possibility that the duration of non-conceptive periods is determined by a necessity to schedule lactation with favorable environmental conditions (i.e., the income-II breeding strategy) must be assessed in future studies including a larger sample of females living under more variable ecological conditions, as food availability at La Flor de Catemaco is high compared with other locations at Los Tuxtlas

TABLE 3 Generalized linear mixed model for variation in interbirth intervals in female mantled howler monkeys

Variable	Estimate	SEM	95%CI	Z	p
Intercept	5.7	0.16	5.4–6.1	36.1	>0.001
Occurrence of lactation	0.9	0.07	0.8–1.1	12.9	>0.001
Thyroid hormone	0.4	0.04	−0.3–(−0.5)	9.1	>0.001
Glucocorticoids	−0.5	0.03	0.5–0.7	19.2	>0.001
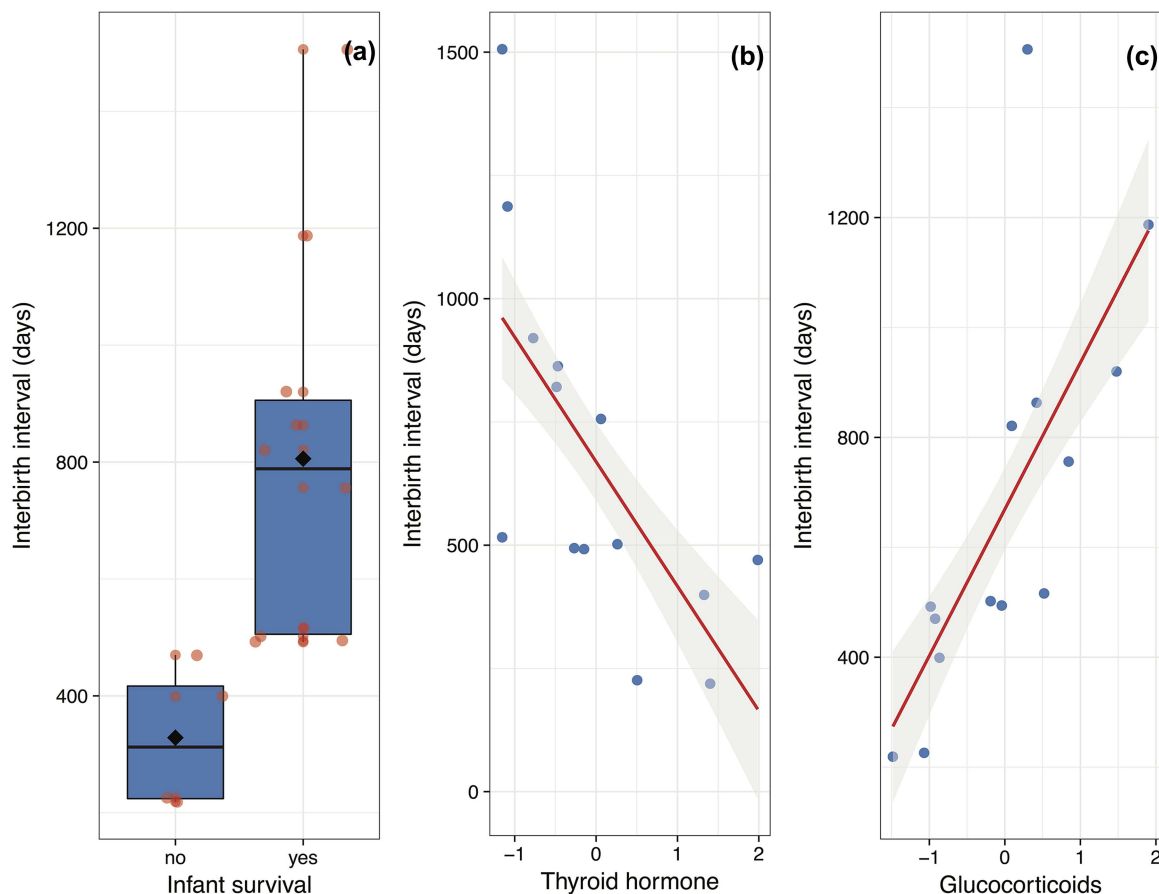
FIGURE 4 Interbirth interval as a function of the survival of the infant at the beginning of the interval (a), mean thyroid hormone (b) and mean glucocorticoid (c) levels during the IBI. $N = 14$ IBI. In A, center lines show the medians, black diamonds are the means, box limits indicate the 25th and 75th percentiles, whiskers extend 1.5 times the interquartile range from the 25th and 75th percentiles, and red dots are data points. In (b) and (c), shaded areas in light gray are the 95% confidence intervals

(Cano-Huertes et al., 2017). Additionally, although glucocorticoids have been linked to energy expenditure in this population (Dias et al., 2017), which was further confirmed in this study by their negative correlation with thyroid hormone levels, they are also associated with other factors, such as social challenges. Participation in agonistic interactions and glucocorticoid levels have been found to co-vary in this and in other howler monkey species (Dias et al., 2017; Gómez-Espinosa et al., 2014; Rangel-Negrín, Coyohua-Fuentes, Chavira-Ramírez, Canales-Espinosa & Dias, 2014). Therefore, variation in female exposure to psychosocial challenges could account for some of the observed variation in both conception probabilities and IBI. For females with longer IBIs, the probabilities of being exposed to such challenges would be higher, which could result in an increase in their mean glucocorticoid levels during IBIs. A systematic sampling of the social behavior of females, and the study of a larger sample of females that allows time-matching the energetic condition of females that differ in IBI length, should allow testing these ideas.

Due to their obvious impact on female fecundity and fertility, gestation, and lactation are the stages of the reproductive process that have traditionally received more attention in studies of female reproductive performance. Still, the cycling stage accounts for a large proportion of IBI in many primate species, and here we demonstrate that the reproductive rates of female mantled howler monkeys are energetically constrained: both the occurrence of conception and IBI are positively affected by female energetic condition.

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