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BRIEF COMMUNICATION

Maternal condition and maternal investment during lactation in mantled howler monkeys

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Abstract

Objectives: Lactation is a costly reproductive state for females, as it may entail decreased body condition, increased morbidity, and increased mortality risk. To offset these costs, mothers should allocate investment in infant care as a function of their physical condition. Here, we assessed the relationship between maternal condition and maternal investment in wild mantled howler monkeys (*Alouatta palliata*) to determine: (1) whether maternal physical condition varied as a function of food availability, activity levels and feeding effort throughout lactation; (2) whether maternal investment was affected by maternal condition and offspring age.

Materials and methods: We studied six adult females while rearing their immature offspring. We determined weekly food availability, C-peptide levels (as a measure of energy balance) in urine samples (306 samples), mothers' time budgets, feeding rates, time spent vigilant, and time spent carrying their offspring (for two years; 600 observation hours).

Results: C-peptide levels were positively related to food availability. Maternal care in terms of vigilance and offspring carrying peaked at early lactation and decreased progressively with offspring age. Carrying was positively related to C-peptide levels and was also influenced by variation in maternal condition throughout lactation.

Discussion: These results converge with previous theoretical and empirical studies on this topic and contribute to the growing evidence that nonhuman primate mothers allocate maternal care based on their current condition to maximize lifetime reproductive success.

KEYWORDS

Alouatta palliata, C-peptide, carrying, infant age, vigilance

1 | INTRODUCTION

Lactation is a costly reproductive stage for female mammals, including primates (Clutton-Brock, 1991). On the one hand, higher caloric demands impose costs in terms of reduced body condition (García, Huffman, & Keiko, 2010), increased morbidity (Archie, Altmann, & Alberts, 2014; McCabe, Emery Thompson, Ehardt, & Gillespie, 2016), and increased mortality risk (Altmann & Alberts, 2005). On the other hand, mothers face costs as a result of tradeoffs among time-budget components to maintain energy balance (e.g., Altmann, 1980; Dias, Rangel-Negrín, & Canales-Espinosa, 2011). Both costs may compromise future reproduction and have a negative influence on female lifetime reproductive success (Trivers, 1972). Therefore, maternal

investment is expected to vary as a function of maternal physical condition (Lee, Majluf & Gordon, 1991).

The prediction that maternal condition and maternal investment are correlated has been seldom tested in nonhuman primates. Three studies conducted with captive primates have shown that maternal investment is a reversed U-shaped function of maternal condition, such that mothers in low and high condition invest less than mothers in intermediate condition (Fairbanks & Hinde, 2013; Fairbanks & McGuire, 1995; Fite, Patera, French, Rukstalis, Hopkins, & Ross, 2005). Such quadratic relationship is explained by the inability of low condition mothers to provide prolonged care for their current offspring (even if early termination of investment entails higher infant mortality) and by the ability of high-condition mothers to maintain their fertility whilst devoting less

time and effort to care for their infants than lower-condition mothers (Fairbanks & McGuire, 1995). Under field conditions, there is evidence that as access to resources increases, mothers terminate investment in current offspring earlier without compromising infant survival (Hauser & Fairbanks, 1988; Lycett, Henzi, & Barrett, 1998). These studies suggest that maternal care is strategically used by mothers to maximize lifetime reproductive success (Fairbanks & Hinde, 2013). Yet, to the best of our knowledge no study has addressed the relationship between a physiological biomarker of maternal condition and maternal care in naturalistic settings.

In this study, we used urinary C-peptide of insulin to perform a preliminary assessment of the relationship between maternal condition and maternal investment in mantled howler monkeys (*Alouatta palliata*). Insulin is involved in short-term responses to the ingestion of carbohydrates and in long-term regulation of energy stores, so it provides a measure of caloric intake and of energy balance. As C-peptide is produced in equimolar amounts as insulin, but is not metabolized as quickly, its measurement provides insight into the rate of insulin production (Emery Thompson, 2017). As other species belonging to this genus, mantled howler monkeys are arboreal quadrupeds with highly selective frugivore-folivore diets (Dias & Rangel-Negrín, 2015). Variation in food availability influences individual behavior (e.g., Clarke, Collins, & Zucker, 2002) and physiology (e.g., Dias, Coyohua-Fuentes, Canales-Espinosa, Chavira-Ramírez, & Rangel-Negrín, 2017), and affects demographic parameters (Cristóbal-Azkarate, Veà, Asensio & Rodríguez-Luna, 2005). Mothers rear their offspring without the help of other group members (Clarke, 1990), and there is evidence that mothers' traveling, feeding effort, vigilance, and time spent carrying their offspring are higher during the first half of the lactation than at other times during the rearing period (Clarke, 1990; Dias et al., 2011; Treves, Drescher, & Snowdon, 2003). This evidence suggests that the energetic investment of mothers in their offspring peaks at early lactation and decreases afterwards until weaning is completed (20 months: Balcells & Baró, 2009). Here, we first analyzed whether maternal condition varied as a function of immature age, food availability, and behavior throughout lactation. Second, we assessed how maternal investment, as proxied by maternal vigilance and immature carrying, was affected by maternal condition and offspring age.

2 | MATERIALS AND METHODS

From August 2013 to July 2015 we studied six adult females belonging to two groups of mantled howler monkeys that lived at La Flor de Catemaco (Los Tuxtlas, Veracruz, México; 18°26′39″ N, 95°02′57″ W). The study site and population have been previously described (e.g., Cano-Huertes et al., 2017; Dias et al., 2017). La Flor de Catemaco is a 250-ha ranch that includes ca. 100 ha of tropical evergreen forest. The age of females varied between 4 and 20 years, and all but one female, were multiparous. No reproductive seasonality has been documented in this population (Cano-Huertes et al., 2017). Following Balcells and Baró (2009), we classified immature individuals as infants 1 (0 to <4 months), infants 2 (4 to <9 months), infants 3 (9 to <15 months), or juveniles 1 (15 to 20 months). Dates of birth of all infants were known with a <7 days error (i.e., on occasions a group

was not sampled for a week). Mothers resume sexual behavior when infants are 3–4 months old, and weaning occurs during the juvenile 1 stage (Balcells & Baró, 2009). At the beginning of the study one female had an infant 1 and another had an infant 2. During the study, another five infants were born.

To determine if maternal physical condition was affected by food availability, each week we assessed the availability of leaves and fruits (the main foods of howler monkeys: Dias & Rangel-Negrín,2015) in 379 trees of species reported as food sources for *Alouatta palliata* using relative abundance scores (Cano-Huertes et al., 2017). These scores were converted to biomass estimations (t/ha of food) using allometric formulae, which in turn allowed calculating weekly total, young leaf, and fruit biomass (described in Cano-Huertes et al., 2017).

To examine the relationship between the behavior of lactating females and their physical condition, we studied their time-budgets and feeding effort using 1-h focal animal sampling with continuous recording during complete days of group follows. Female behavior was categorized as resting, feeding, moving, and socializing. To determine feeding effort, during feeding we recorded the number of bites, defined as each occasion on which food was put into the mouth during a feeding episode (Reynoso-Cruz, Rangel-Negrín, Coyohua-Fuentes, Canales-Espinosa, & Dias, 2016). During the 24 study months, we completed 600 observation hours, with a mean ± SE of 100 ± 29.7 hr per female, and of 150 ± 13.5 hr per immature category (Table 1).

To study the physical condition of mothers, we measured urinary C-peptide levels (Emery Thompson, 2017) via radioimmunoassay with a commercial kit (Human C-Peptide, Merck Millipore, Billerica, MA). We have previously described our collection, preservation, processing, and assay procedures, as well as the biological validation of our protocol (Cano-Huertes et al., 2017). The interassay coefficient of variation (CV) of controls for the C-peptide assay was 9.5% ($N = 10$), and intra-assay CV was 6.3% ($N = 10$). C-peptide measurements were corrected for creatinine concentrations and expressed as pg/mg of creatinine. Females were sampled every two weeks, and we analyzed a total of 306 urine samples, with a mean ± SE of 76.5 ± 4.9 samples per immature category, and 51 ± 14.8 samples per female.

To assess maternal care, during focal samples we recorded whether mothers were vigilant by instantaneous recording every 15 min during focal samples. Females were recorded as vigilant if their heads were up, their eyes were open, and their attention was not focused on another activity, such as feeding, moving, or socializing (Barrett, Halliday & Henzi, 2006). During focal samples, we also recorded the time mothers spent carrying their immature offspring. Increased vigilance and time spent carrying equals high maternal investment.

For each week of observations, we calculated mean values of the following variables for each mother ($N = 118$ weeks): total biomass, young leaf biomass, and fruit biomass; an activity index to estimate activity level calculated as the sum of time spent feeding, moving, and socializing divided by time spent resting (Cavigelli, 1999); feeding rate, calculated as the number of food bites divided by feeding time; C-peptide levels; the proportion of time spent vigilant; and proportion of time spent carrying immature offspring.

Biomass measures were collinear in this model (i.e., had variance inflation factors >5), so we reduced them to a subset of orthogonal factors using principal components analysis. This analysis resulted in a

TABLE 1 Number of sampling weeks and observation hours per mother according to the age category of her offspring

Female	Infant 1		Infant 2		Infant 3		Juvenile 1	
	Weeks	Hours	Weeks	Hours	Weeks	Hours	Weeks	Hours
1	6	28	9	46	8	39	6	29
2	5	23	8	34	10	49	6	26
3[a]	2	10	0	0	0	0	0	0
4	4	24	6	39	9	45	9	60
5	6	23	9	53	8	35	6	32
6[b]	1	5	0	0	0	0	0	0
Total	24	113	32	172	35	168	27	147

[a]This female's infant was born near the end of the study.
[b]This female's infant died at 1 week of age.

single component with an eigenvalue of 3.1 that explained 80.9% of the variance in the original variables, and was positively correlated with total food biomass ($r = 0.97$), fruit biomass ($r = 0.95$), and young leaf biomass ($r = 0.87$). This component, named food biomass, was used in models of C-peptide and maternal behavior.

To determine if maternal physical condition was affected by immature age, food availability, activity levels, and feeding effort, we used a linear mixed model (LMM), in which C-peptide levels were the dependent variable, total plant biomass, young leaf biomass, fruit biomass, activity index, and feeding rate were fixed predictors, and mother identity was a random factor to account for the repeated sampling of the same mothers in different weeks.

To analyze variation in maternal care, we also used LMM, with the proportion of time spent vigilant and time spent carrying immature offspring as the dependent variables in two different models, C-peptide levels, immature category, and the interaction between C-peptide levels and immature category as fixed predictors, and mother identity as a random factor. We additionally added sampling time per mother per week as an offset variable to account for variable sampling effort among mothers/weeks. Model fit was assessed via coefficients of determination. Significant categorical and interaction factors were analyzed *post-hoc* with Tukey contrasts. All predictors had variance inflation factors ≤ 1.5, indicating no multicollinearity (Neter, Wasserman, & Kutner, 1990). Our models were a better fit for dependent variables than null models including only the intercept and random factor (likelihood ratio tests: C-peptide $\chi^2 = 115.6$, d.f. = 6, $p < .001$; vigilance $\chi^2 = 38.0$, d.f. = 7, $p < .001$; carrying $\chi^2 = 137.3$, d.f. = 7, $p < .001$). We diagnosed model validity by inspection of the distribution of residuals and quantile-quantile plots to verify normality, and of residuals plotted against predicted values to assess homogeneity. We performed all tests in R 3.4.3. (R Core Team, 2017) with the packages lmr4 (Bates, Maechler, Bolker, & Walker, 2015), car (Fox & Weisberg, 2011), r2glmm (Jaeger, 2017), usdm (Naimi, Hamm, Groen, Skidmore, & Toxopeus, 2014), and multcomp (Hothorn, Bretz, & Westfall, 2008).

3 | RESULTS

The model of variation in C-peptide levels of mothers was significant (Table 2). C-peptide levels were lower in mothers of infants 1 than in mothers of immatures of all other categories, and lower in mothers of

juveniles 1 than in mothers of infants 2 ($p < .01$ for all pairwise comparisons Figure 1a). C-peptide levels were also higher when food biomass was higher (Figure 1b), but were unaffected by feeding rate and activity levels.

The proportion of time mothers dedicated to vigilance was affected by immature category, but not by either C-peptide or by the interaction between immature category and C-peptide (Table 3). Specifically, mothers of infants 1 spent more time vigilant than mothers of other immature classes, and mothers of infants 2 were more vigilant than mothers of juveniles 1 ($p < .01$ for all pairwise comparisons; Figure 2).

Variation in time mothers spent carrying their immature offspring was explained by a model including immature category, C-peptide levels, and the interaction between C-peptide levels and immature age (Table 4). Mothers spent more time carrying infants 1 than offspring in all other categories, and infants 2 were more carried than infants 3 and juveniles 1 ($p < .01$ for all pairwise comparisons; Figure 3a). Carrying time was also higher when mothers had higher C-peptide levels (Figure 3b). Additionally, the relationship between C-peptide and time spent carrying was affected by immature age, such that whereas no relationship was found for infants 1, a positive relationship existed in mothers of infants 2 and infants 3, and a negative relationship was recorded for mothers of juveniles 1 ($p < .05$ for all comparisons; Figure 3c).

4 | DISCUSSION

Evolutionary theory posits that mothers should allocate care as a function of their lifetime reproductive success (Clutton-Brock, 1991;

TABLE 2 Linear mixed model ($R^2 = 0.62$) of factors influencing maternal C-peptide levels in female mantled howler monkeys

Predictor	β	SE	t	p
Intercept	41.3	4.2	9.9	<.001
Infant age − Infant 2	11.5	3.9	2.9	.004
Infant age − Infant 3	13.9	3.8	3.6	<.001
Infant age − Juvenile 1	1.0	3.6	0.3	.773
Food biomass	7.1	0.8	8.6	<.001
Feeding rate	1.4	3.8	0.3	.730
Activity	0.1	0.5	0.2	.869

Comparisons of infant age are done against the Infant 1 category.
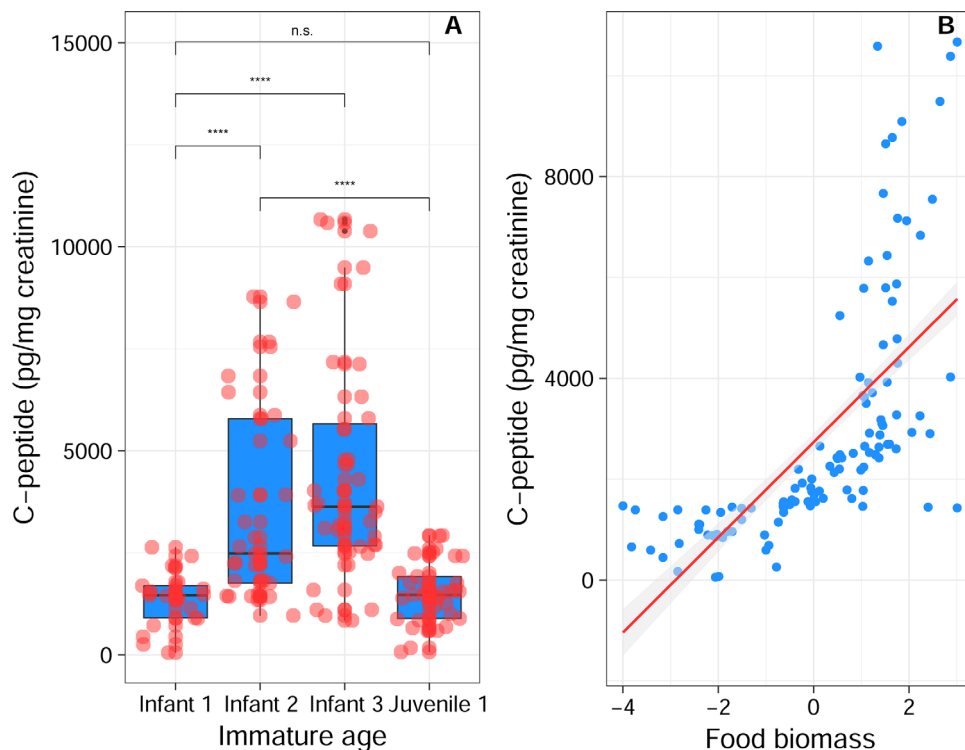
FIGURE 1 The relationship between maternal urinary C-peptide levels and both immature age (a), and available food biomass (b) and in mantled howler monkeys. In A, red dots are individual data points, center lines show the medians, box limits indicate the 25th and 75th percentiles, whiskers extend 1.5 times the interquartile range from the 25th and 75th percentiles. n.s. is non-significant, **** $p < .0001$. In B blue dots are individual data points, and area shaded in gray represents 95% confidence intervals

Trivers, 1972). Because lactation is a costly reproductive state that impacts female physical condition, morbidity, and mortality (Altmann & Alberts, 2005; Archie et al., 2014; García et al., 2010), mothers are expected to vary investment in care according to their physical condition (Lee et al., 1991). In our study, maternal care by mantled howler monkeys peaked during early lactation and decreased progressively with offspring age. Offspring carrying was positively related to maternal physical condition (which in turn increased with increasing food availability), and was also influenced by variation in maternal condition throughout lactation. A limitation of this study is that we could only sample a small number of females, due to the difficulties involved in following and collecting urine samples from arboreal primates. Nevertheless, the evidence that we obtained on the variation in maternal care is consistent with evolutionary theory,

converges with previous studies conducted with captive nonhuman primates (Fairbanks & Hinde, 2013; Fairbanks & McGuire, 1995; Fite et al., 2005), and therefore offers insight into the reproductive strategies of female primates.

To offset the costs of lactation, females may eat longer, faster, and/or "smarter" (e.g., foods richer in key nutrients) (Lee, 1987).

TABLE 3 Linear mixed model ($R^2 = 0.28$) of factors influencing maternal vigilance time in female mantled howler monkeys

Predictor	β	SE	t	p
Intercept	1.1	0.5	2.28	.022
C-peptide	0.2	0.7	0.29	.767
Infant age – Infant 2	−0.85	0.5	−1.69	.091
Infant age – Infant 3	−1.24	0.5	−2.47	.013
Infant age – Juvenile 1	−1.52	0.6	−2.68	.007
C-peptide × Infant age – Infant 2	−0.15	0.7	−0.21	.838
C-peptide × Infant age – Infant 3	−0.27	0.7	−0.39	.699
C-peptide × Infant age – Juvenile 1	−0.07	0.8	−0.08	.933

Comparisons of infant age are done against the Infant 1 category.
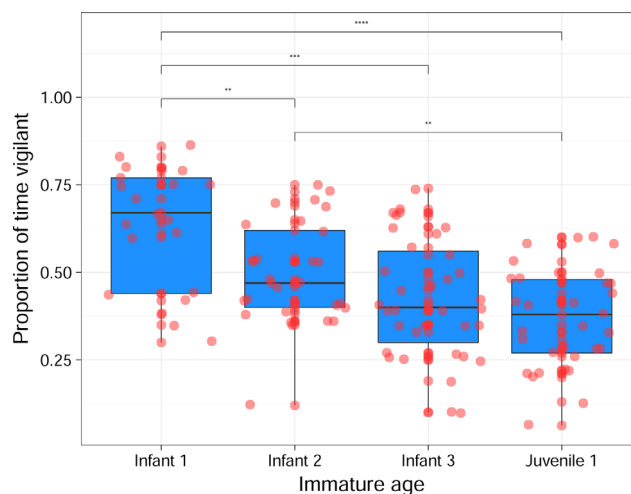
FIGURE 2 Variation in maternal vigilance as a function of immature category in mantled howler monkeys. Red dots are individual data points, center lines show the medians, box limits indicate the 25th and 75th percentiles, whiskers extend 1.5 times the interquartile range from the 25th and 75th percentiles. ** $p < .01$, *** $p < .001$, **** $p < .0001$

TABLE 4 Linear mixed model ($R^2 = 0.70$) of factors influencing time mothers spent carrying immatures in female mantled howler monkeys

Predictor	β	SE	t	p
Intercept	1.86	0.5	3.75	<.001
C-peptide	−0.02	0.7	−0.03	.975
Infant age − Infant 2	−1.82	0.5	−3.44	<.001
Infant age − Infant 3	−3.01	0.5	−5.68	<.001
Infant age − Juvenile 1	−3.26	0.6	−5.42	<.001
C-peptide × Infant age − Infant 2	1.23	0.8	1.63	.006
C-peptide × Infant age − Infant 3	0.71	0.7	0.95	.044
C-peptide × Infant age − Juvenile 1	−0.63	0.9	−0.69	.487

Comparisons of infant age are done against the Infant 1 category.

They may also decrease energy expenditure by increasing time spent resting (e.g., Barrett et al., 2006; Dias et al., 2011). Maternal physical condition was only related to food availability. This result suggests that either our measures of activity levels and feeding effort did not capture the subtleties of behavioral variation among lactating females, or that females could be eating "smarter." That is, they ingested more key nutrients and/or energy when they were available while keeping feeding time and rate the same. Future studies should aim at measuring nutrient and energy intake by mothers throughout lactation.

The decrease in maternal vigilance as offspring grew older was independent of C-peptide levels, suggesting that in this species the trade-off of vigilance for other time-budget components does not affect maternal physical condition. This is consistent with evidence from other primate species (e.g., Barrett et al., 2006). It is possible that mothers of young infants are able to allocate time to vigilance without incurring notable energy costs due to the conservative time budgets of this species, which include up to 80% of daylight time resting (Di Fiore, Link, & Campbell, 2010). Still, vigilance varies according to factors different from immature protection (e.g., Treves, 2000), so its value as a predictor of maternal investment remains to be demonstrated in this species.

In contrast with vigilance, carrying entailed energy costs that varied throughout lactation. Mothers rearing infants 1, in spite of having overall lower C-peptide levels than mothers rearing offspring of other immature categories, did not vary carrying effort according to their physical condition, probably because they could not as infants 1 cannot be parked and are not carried by other group members (Clarke, 1990). Mothers rearing infants 2 and 3, on the contrary, spent more time carrying when they had higher C-peptide levels, confirming that the degree of maternal care depends on maternal condition at least for these age categories (Fairbanks & Hinde, 2013). Finally, mothers that had high physical condition while rearing juveniles 1 carried them less often. This result suggests that high-quality mothers may terminate investment earlier than other mothers without risking the survival probabilities of their offspring, as found in other studies (Fairbanks & McGuire, 1995; Fairbanks & Hinde, 2013).

In summary, based on a robust measure of maternal physical condition and on two years of field observations of individually
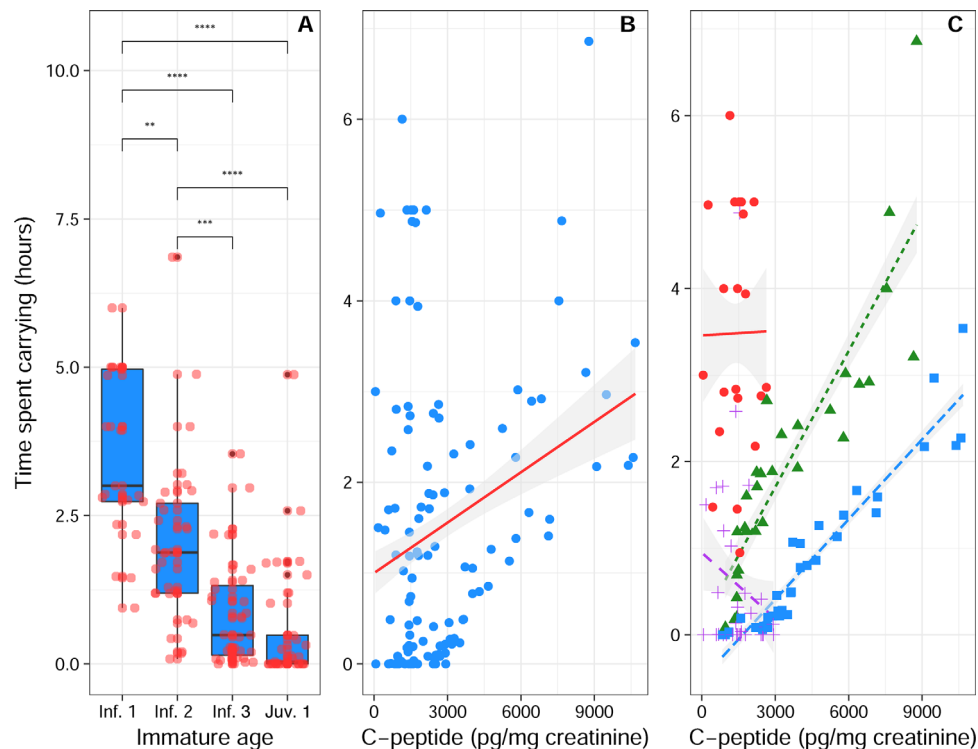
FIGURE 3 Factors affecting maternal carrying in mantled howler monkeys: (a) immature category. Center lines show the medians, box limits indicate the 25th and 75th percentiles, and whiskers extend 1.5 times the interquartile range from the 25th and 75th percentiles. ** $p < .01$, *** $p < .001$, **** $p < .0001$; (b) maternal urinary C-peptide levels. Area shaded in gray represents 95% confidence intervals; (c) the interaction between maternal urinary C-peptide levels and immature age. Areas shaded in gray represent 95% confidence intervals. Red circles = infants 1; green triangles = infants 2; blue squares = infants 3; purple sum signs = juveniles 1

recognized females, our study indicates that maternal physical condition is associated with one aspect of maternal care (i.e., carrying) in mantled howler monkeys, but this association is modulated by offspring age. By supporting theoretical expectations and converging with the findings of other empirical studies, our results contribute to the growing evidence that nonhuman primate mothers allocate maternal care strategically to maximize lifetime reproductive success.

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