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Preliminary Evidence of Maternal Care Styles in Mantled Howler Monkeys (*Alouatta palliata*)

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Abstract

Parental care strategies are adaptations shaped by evolutionary pressures to maximize offspring survival while balancing current and future reproductive investment. Maternal care styles, which are consistent patterns of behavior that vary among individuals, have been well-documented in catarrhines but remain poorly understood in platyrrhines. Furthermore, while previous studies have documented that maternal behaviors change as infants develop, whether individual maternal styles remain consistent or shift across infant developmental stages remains largely unexplored. This represents a critical gap, because understanding the interaction between maternal styles and infant age could reveal whether mothers maintain fixed behavioral phenotypes or demonstrate flexible responses to changing developmental needs. We investigated whether wild mantled howler monkeys (*Alouatta palliata*) show distinct maternal care styles that change across infant development. Using an age-specific analytical approach, we examined whether maternal behavior is organized into distinct styles during each of early, middle, and late infant development. We observed 16 mother-infant dyads in four groups at three sites in Los Tuxtlas, Mexico, collecting 743 hours of focal observations over 2 years. Using robust principal component analysis and bootstrap-validated cluster analysis, we identified three distinct maternal styles during early infancy (*Minimal-investment*, *High investment*, and *Proximity-focused*), three styles during middle infancy (*Minimal-investment*, *High-support*, and *Mixed-investment*), and two styles during late infancy (*Minimal-investment* and *Selective-support*). We found minimal consistency in individual maternal styles across infant development stages, with infant age significantly explaining behavioral variance whereas maternal identity did not. Our results offer preliminary evidence that mantled howler monkey mothers strategically adjust care patterns in response to infant developmental needs rather than maintaining consistent individual styles. If such dynamic adjustment allows for the successful balancing of the competing demands of ensuring current offspring survival and maintaining capacity for future reproduction, our results contribute to the understanding of the evolution of maternal investment strategies in primates.

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Keywords *Alouatta* · Maternal style · Parental behavior · Platyrrhines · Protection · Rejection

Resumen

Las estrategias de cuidado parental son adaptaciones moldeadas por presiones evolutivas para maximizar la supervivencia de las crías a la vez que se equilibra la inversión reproductiva actual y futura. Los estilos de cuidado materno, que son patrones consistentes de comportamiento que varían entre individuos, han sido bien documentados en los catarrinos, pero siguen siendo poco conocidos en los platirrinos. Además, aunque estudios previos han documentado que los comportamientos maternos cambian a medida que los infantes se desarrollan, sigue en gran medida sin explorarse si los estilos maternos individuales permanecen constantes o cambian a lo largo de las etapas de desarrollo de los infantes. Esto representa una laguna crítica, ya que comprender la interacción entre los estilos maternos y la edad de los infantes podría revelar si las madres mantienen fenotipos de comportamiento fijos o demuestran respuestas flexibles a las necesidades cambiantes del desarrollo. Observamos 16 díadas madre-infante en cuatro grupos en tres sitios en Los Tuxtlas, México, recolectando 743 horas de observaciones focales durante dos años. Mediante un análisis robusto de componentes principales y un análisis de conglomerados validado por bootstrap, identificamos tres estilos maternos distintos durante la primera infancia (*Inversión-mínima*, *Alta-inversión* y *Centrado-en-la-proximidad*), tres estilos durante la infancia media (*Inversión-mínima*, *Alto-apoyo* e *Inversión-mixta*) y dos estilos durante la infancia tardía (*Inversión-mínima* y *Apoyo-selectivo*). Encontramos una consistencia mínima en los estilos maternos individuales a través de las etapas de desarrollo infantil, con la edad infantil explicando significativamente la varianza conductual mientras que la identidad materna no lo hizo. Nuestros resultados aportan evidencia preliminar de que las madres de los monos aulladores de manto ajustan estratégicamente los patrones de cuidado en respuesta a las necesidades de desarrollo del infante en lugar de mantener estilos individuales consistentes. Si este ajuste dinámico permite equilibrar con éxito las demandas contrapuestas de asegurar la supervivencia de la descendencia actual y mantener la capacidad para la reproducción futura, nuestros resultados contribuyen a la comprensión de la evolución de las estrategias de inversión materna en los primates. ***The translated abstract was not copy edited by Springer Nature.**

Palabras clave *Alouatta* · Cuidado parental · Estilo materno · Platirrinos · Protección · Rechazo

Introduction

Parental care is a fundamental aspect of reproduction that significantly influences the evolution, ecology, and behavioral ecology of animals. It encompasses a wide range of behaviors through which parents contribute to the survival and development of their offspring (Clutton-Brock, 1991; Royle et al., 2012). From

an evolutionary perspective, parental care strategies are shaped by natural selection to maximize reproductive success, with parental investment theory explaining how parents optimize the allocation of limited resources across current and future offspring (Stearns, 1992; Trivers, 1972). This theoretical framework helps explain the considerable variation observed in maternal investment across primate species with different life history patterns (Altmann, 1980; Lee, 1996). Ecologically, parental care affects population dynamics and species interactions by influencing offspring survival and fitness (Kirkpatrick & Lande, 1989). Studying parental care also provides insight into the adaptive responses of animals to their environment, including resource availability, predation risk, and social structure (Smiseth et al., 2012). Variation in parental care strategies both within and among species has profound implications for understanding how animals balance the costs and benefits of investing in their young (Royle et al., 2012).

Maternal care style is a key concept for understanding variation in rearing behavior. Maternal care style refers to consistent patterns of maternal behavior that differ among individuals and reflect distinct rearing strategies (Fairbanks, 1996; Hinde & Spencer-Booth, 1971; Maestripieri, 1999). These styles have traditionally been defined through the intersection of two independent dimensions of maternal care, protectiveness and rejection, giving four styles: protective (high protectiveness, low rejection); controlling (high protectiveness and rejection); rejecting (low protectiveness, high rejection); and laissez-faire (low protectiveness and rejection) (Maestripieri, 1999). Maternal care styles diverge in terms of the degree to which mothers provide support, control, and opportunities for infant independence (Bardi & Huffman, 2002). Assessment of maternal care style involves quantifying specific maternal behaviors, such as proximity maintenance, carrying, rejection, and food sharing (Fairbanks & McGuire, 1987). Importantly, longitudinal studies have shown that individual mothers tend to show consistent maternal styles across different offspring, suggesting that maternal care style is a stable behavioral trait influenced by both genetic and environmental factors (Berman, 1980; Fairbanks, 1996; Revathe *et al.*, 2024).

Research on maternal care styles in primates has focused primarily on catarrhine monkeys, where studies have revealed considerable variation in maternal behavior. For example, in rhesus macaques (*Macaca mulatta*), maternal styles range from restrictive, in which mothers tightly control infant movements, to relaxed styles that promote independence (Hinde & Spencer-Booth, 1968; Maestripieri, 1994). Similar patterns are observed in vervet monkeys (*Chlorocebus pygerythrus*), where maternal rank and social context influence rearing strategies (Fairbanks & McGuire, 1987). A study of capuchin monkeys (*Sapajus* spp.) identified distinct maternal styles along a continuum from permissive (laissez-faire) to protective, with mothers showing consistent patterns across successive infants (Verderane & Izar, 2019). However, maternal behaviors did not always combine as predicted by traditional models developed for catarrhines, suggesting that these may not fully capture the complexity of maternal care styles in platyrrhines due to differences in ecological constraints and social systems (Verderane & Izar, 2019). For instance, platyrrhine societies are less despotic and dominance relationships are more egalitarian compared to catarrhines, which may result in a

less risky social context for infants and thus affect maternal care strategies (Verderane & Izar, 2019).

While maternal styles have been well-characterized, less attention has been paid to how these styles vary across infant development. Maternal behaviors universally change as infants mature, for example, through decreases in contact, proximity, and carrying but increases in rejection (Arbaiza-Bayona et al., 2022; Förster & Cords, 2002; Li et al., 2013; Roura-Torres et al., 2025). However, whether mothers maintain consistent styles while adjusting the absolute levels of behavior, or whether the styles themselves transform across development, remains unclear. This distinction is crucial as stable styles would suggest inherent maternal phenotypes, while age-dependent style changes would indicate strategic flexibility in response to infant needs.

Howler monkeys (*Alouatta* spp.) are a particularly interesting case for studying maternal care in platyrrhines. These highly arboreal primates are characterized by a frugivorous-folivorous diet, small groups, and a low-energy lifestyle (Di Fiore & Campbell, 2007). Their arboreal lifestyle presents challenges for infant development, as young monkeys must navigate complex three-dimensional environments while facing increased risks of falls and predation. Maternal care in howler monkeys involves prolonged physical contact, including extensive carrying and a gradual reduction in direct maternal support as infants develop (Arroyo-Rodríguez et al., 2007; Clarke, 1990; Pavé et al., 2010). Variation in maternal behavior has been reported in black and gold (*A. caraya*) and mantled howler monkey (*A. palliata*) mothers, particularly in carrying patterns and responses to infant distress calls, suggesting individual differences in maternal care strategies (Dias et al., 2018; Pavé et al., 2015). These observations of differential maternal behaviors, such as differences in rejection rates and infant transport, suggest the potential for distinct maternal care styles in this genus. However, there is a notable gap in the literature regarding whether these behavioral patterns represent discrete styles or a more flexible continuum, highlighting the need for focused studies on maternal care style in howler monkeys (Raguet-Schofield & Pavé, 2015).

We aimed to explore the existence of maternal care styles in wild mantled howler monkeys. We hypothesized that howler monkey mothers exhibit maternal care styles that change across infant development, with styles emphasizing physical protection more prevalent with younger infants and styles promoting independence more common with older infants. We predicted that (1) discrete, identifiable maternal care styles would emerge at each infant age, and (2) the behavioral composition of these styles would differ across infant ages in ways that correspond to changing infant developmental needs.

Methods

Study Sites and Subjects

We studied wild mother-infant dyads living in four groups of mantled howler monkeys at three sites in Los Tuxtlas (southeastern Veracruz, México): La Flor de

Catemaco (18°26′18″ N, 95°03′12″ W); Balzapote (18°36′38″ N, 95°04′11″ W); and Cerro del Borrego (18°38′32″ N, 95°05′30″ W) (Table I). All subjects were habituated to the presence of researchers (these groups have been studied for more than 20 years), and we identified individuals based on their natural physical characteristics.

We studied 11 mothers that had associated infants during the study. Five females were observed in two different rearing processes, resulting in a total of 16 observed mother-infant dyads (Table II). We classified individuals younger than 15 months old in three developmental stages: infant 1 (0–3 months, early lactation); infant 2 (4–8 months, middle lactation); infant 3 (9–14 months, late lactation) (Balcells & Veà, 2009). We determined offspring age through long-term demographic records (n = 3), observation of births (n = 10), or observation of physical characteristics (n = 3), such as coat color and size, (Balcells & Veà, 2009), which allow for accurate age estimations.

Behavioral Sampling

From September 2021 to September 2023, we followed study groups for 8 hr per day, during which a single observer used focal animal sampling with continuous recording to study mothers with infants. In each focal sample we recorded the duration of all mother-infant interactions (Table III). We stopped focal samples when infants were out of sight and resumed them when they became visible. If mothers or infants were out of sight for more than 1 hr, we sampled another focal subject. Owing to the challenges associated with finding and following the focal individuals, each day we tried to sample mothers for as long as possible, resulting in high variation in focal sample duration: mean ± standard deviation [SD] = 3.8 ± 1.5 hr, range = 1.1–7.0 h (n = 743 h of focal observations). We collected data for each dyad on a mean ± SD of 4.1 ± 1.3 days per infant age category and collected a minimum of 5 hr of focal observations per mother-infant dyad per infant age category.

Data Analysis

We never observed mothers grooming their infants. Except for carrying and waiting, most instances of maternal care behaviors were brief (<2 s). We therefore analyzed these behaviors as rates by dividing the number of events by the

Table I Composition of the mantled howler monkey groups studied at Los Tuxtlas (Mexico) from September 2021 to September 2023

Composition	La Flor 1	La Flor 2	Balzapote	Cerro del Borrego
Adult females*	4–6	5	4	8
Adult males	3–4	4	2–3	10
Juveniles	8–11	0	1–2	3
Infants	2–4	1	2–5	2–4
Total group size	17–25	10	9–14	23–24

* Group size and composition varied (showed with dashes) due to migration, births, and deaths.

Table II Mother-infant dyads and observation effort for mantled howler monkeys studied at Los Tuxtlas (Mexico) from September 2021 to September 2023

Site	Group	Year of observation	Dyad (mother-infant)	Observation effort (hr)			
				Age 1	Age 2	Age 3	Total
La Flor de Catemaco	1	2022	H1-C1	5.4	5.8		11.2
	2	2021-2022	HD-C1	5.0	6.9		11.9
	2	2021-2022	HPM-C1	6.3	7.5	10.5	24.3
	2	2022-2023	HPM-C2	26.0	34.6	20.4	81.0
	2	2022-2023	HPG-C1	13.3	55.4	33.1	101.8
	2	2022-2023	HA-C1	29.4	44.3	39.2	112.9
	2	2023	HA-C2	33.6			33.6
Balzapote	B2	2021-2022	HB1-C1*		15.3	15.8	31.1
	B2	2023	HB1-C3	10.4	17.5		27.9
	B2	2022	HB2-C1*	24.2	23.7	14.5	62.4
	B2	2023	HB2-C2	15.4	37.7		53.1
	B2	2022	HB3-C1	22.3			22.3
	B2	2023	HB3-C2	40.3			40.3
	B2	2022-2023	HB4-C1	20.4	34.9	47.8	103.1
Cerro del Borrego	Cerro del Borrego	2022	HCB1-C1	13.8			13.8
	Cerro del Borrego	2022	HCB2-C1*		12.6		12.6
Total				241.4	306.2	195.4	743.0

*We estimated the age of these subjects via physical characteristics at the beginning of observations.

observation time per mother. For carrying and waiting we calculated both proportions of time (i.e., total time spent in each behavior divided by observation time per mother) and rates. Calculation of behavioral rates and proportions accounted for variation in sampling effort among dyads and infant ages.

We conducted separate analyses for each of the three infant age categories to ensure that any maternal care styles we identified reflected age-specific behavioral patterns rather than artifacts of unbalanced sampling. For each age category, we used Robust Principal Component Analysis (RPCA) using Hubert's method with minimum covariance determinant (MCD) estimation ($\alpha = 0.75$) through the "robustbase" package in R (R Core Team, 2025). We chose RPCA over standard PCA to minimize the influence of potential outliers in our small sample, which was particularly important given the uneven sampling across mother-infant dyads. Prior to RPCA, we standardized all behavioral variables to z-scores, using robust scaling based on medians and median absolute deviations rather than means and standard deviations. We retained principal components with eigenvalues greater than 1.0 following the Kaiser criterion. We assessed the statistical significance of the component structure using permutation tests (PERMANOVA, 1,000 permutations) using the "vegan" package and Gower distance metrics, which are

Table III Maternal behaviors observed in mantled howler monkey females studied at Los Tuxtlas (Mexico) from September 2021 to September 2023

Behavior	Description	Source
Approach	The mother moves from more than 1 m to less than 1 m from the infant	Förster & Cords, 2002
Break contact	The mother terminates physical contact	Pavé et al., 2015
Bridge	The mother helps the infant to cross a gap in the canopy	Clarke et al., 1998
Carry	The mother carries the infant in the back or belly during locomotion	Clarke et al., 1998
Food sharing	The mother shares solid food with the infant	Verderane & Izar, 2019
Groom	The mother touches with its hands some part(s) of the body of the infant, splitting delicately apart the hair, and with visual attention	Dias & Rangel-Negrín, 2015
Leave	The mother moves from less than 1 m to more than 1 m from the infant	Förster & Cords 2002
Make contact	The mother moves toward the infant until they are in physical contact	Pavé et al., 2015
Reject	The mother pushes her infant away, removes the infant from her back, moves away, or obstructs access to the nipple with an arm	Pavé et al., 2010
Restrain	The mother holds her infant tightly with her hands as the infant tries to move or squirm away, or by pulling the infant back toward her if it manages to get away	Schino et al., 1995
Retrieve	The mother picks up her infant	Maestripieri, 2001
Wait	During locomotion, the mother stops moving to wait for her infant to make contact and carrying it	This study

particularly robust for mixed data types and handle missing values effectively (D'Orazio, 2021). These tests generate null distributions by randomly permuting the original data to determine whether the observed component structure could have arisen by chance.

We performed cluster analysis on the robust principal component scores using hierarchical clustering with Ward's method and Manhattan distance metrics. We chose Manhattan distance over Euclidean distance due to its reduced sensitivity to outliers and greater appropriateness for behavioral data with zero values. To determine the optimal number of clusters for each age category and assess cluster stability despite small sample sizes, we used bootstrap validation (999 iterations) following the approach of Hennig (2007) using the "fpc" package. For each bootstrap iteration, we resampled the data with replacement, performed clustering, and calculated Jaccard similarities between the bootstrap-generated cluster solution and the original clusters. We considered Jaccard similarity values above 0.75 indicative of stable clusters. We selected the number of clusters that maximized both silhouette width and bootstrap stability. After identifying distinct maternal care styles for each infant age, we characterized these styles based on their behavioral compositions and validated their distinctiveness using PERMANOVA (999 permutations) on the original behavioral variables.

To assess stability in maternal care styles across infant development, we calculated Cohen's kappa using the "irr" package. We used PERMANOVA (999 permutations) to assess if PCA scores varied with infant age and with maternal identity and infant age (i.e., whether individual mothers maintain distinct behavioral profiles in the reduced dimensional space while accounting for the longitudinal structure of data). A more balanced comparison would test both factors while controlling for the other, but the structure and size of our dataset precluded this approach.

Ethical note

We complied with The International Primatological Society Code of Best Practices for Field Primatology. Our research conformed with the Mexican Law (NOM-059- SEMARNAT- 2010) and was approved by permits SEMARNAT SGPA/DGVS/04015/21 and SGPA/DGVS/00278/22.

Data Availability The datasets used in this study are not publicly available due to an agreement with Universidad Veracruzana (UV) but are available from the corresponding author on reasonable request and with permission from UV.

Conflict of Interest The authors declare that they have no conflict of interest.

Results

Robust Principal Component Analysis by Infant Age

Age 1 (0–3 months)

For mothers with infants in age category 1 (n = 14 dyads), RPCA identified four components with eigenvalues >1 that together explained 74.9% of variance in maternal behaviors. A permutation test showed that this structure was significantly different from random (p = 0.002). The first component was strongly associated with retrieving, carrying frequency, restraining, and waiting frequency (Table IV). This component appears to capture a behavioral syndrome of active physical management versus passive monitoring. The second component was primarily defined by approach, rejection, making contact, and restraining behaviors, representing a complex proximity regulation syndrome that integrates both affiliative and limiting behaviors. The third component was associated with breaking contact, making contact, waiting frequency, and rejection, suggesting strategies for managing contact dynamics. The fourth component was characterized by bridging and food sharing, representing direct assistance and provisioning behaviors.

Age 2 (3–8 months)

For mothers with infants in age category 2 (n = 11), RPCA identified four components with eigenvalues >1 that explained 81.2% of variance. A permutation test showed that this structure was significant ($p < 0.001$). The behavioral loading patterns differed significantly from age 1 (PERMANOVA, F = 4.28, p = 0.003) and we did not observe food sharing at this infant age category. The first component was associated with leaving, waiting frequency, carrying frequency, and bridging (Table IV). This component captures a behavioral syndrome of facilitating independence while maintaining readiness to assist. The second component showed the clearest separation between protective behaviors (positive loadings: retrieving, carrying duration, making contact) and rejection behaviors (negative loadings: rejection, breaking contact), suggesting that a protection-rejection dimension emerges more clearly during middle infancy. The third component was positively associated with waiting duration and approach, and negatively associated with carrying frequency, representing alternative supervision strategies. The fourth component was characterized by negative loadings of restraining and waiting frequency, and positive loadings of rejection, representing behavioral packages related to infant autonomy.

Age 3 (9–14 months)

For mothers with infants in age category 3 (n = 7), RPCA identified three components with eigenvalues >1 that explained 78.3% of variance. A permutation test showed that this structure was significant (p = 0.007). Loading patterns changed

Table IV Component loadings of each behavioral variable with eigenvalue >1 in a robust Principal Components Analysis of maternal behaviors by infant age category, in mantled howler monkey females at Los Tuxtlas (Mexico) from September 2021 to September 2023

Behavior	Age 1 (0–3 months)				Age 2 (4–8 months)				Age 3 (9–14 months)		
	PC1	PC2	PC3	PC4	PC1	PC2	PC3	PC4	PC1	PC2	PC3
Explained variance (%)	36.2	27.8	12.3	8.4	33.5	22.1	15.7	9.9	37.2	24.5	16.6
Eigenvalue	3.9	3.2	2.9	1.9	4.4	3.2	2.2	1.3	3.7	2.4	1.9
Approach	0.05	0.44	0.00	0.21	0.25	−0.02	0.55	0.00	0.04	0.10	0.14
Break contact	−0.12	0.38	0.48	0.16	0.31	−0.35	−0.05	0.25	0.43	0.00	−0.20
Bridge	0.03	0.02	0.31	−0.70	0.31	−0.32	0.23	−0.20	0.06	−0.46	0.26
Carry duration	−0.34	−0.06	−0.21	0.09	0.26	0.45	−0.15	0.02	−0.46	0.13	0.11
Carry frequency	−0.42	−0.20	−0.17	0.15	0.37	0.06	−0.30	0.27	0.32	0.41	0.30
Food sharing	0.18	−0.30	0.25	0.61	—	—	—	—	—	—	—
Leave	0.01	0.11	0.05	0.03	0.44	−0.06	0.00	0.19	0.43	−0.06	0.04
Make contact	0.33	0.40	−0.39	0.15	0.23	0.43	0.18	0.16	0.12	0.18	−0.67
Reject	−0.25	0.40	0.33	0.12	0.24	−0.36	−0.20	0.32	0.47	−0.01	−0.10
Restrain	0.37	−0.39	0.20	0.04	0.21	−0.20	−0.06	−0.70	—	—	—
Retrieve	0.47	0.20	−0.30	−0.07	0.24	0.46	0.08	−0.12	0.09	−0.23	−0.16
Wait duration	0.00	0.00	0.01	−0.01	0.06	−0.05	0.63	0.09	0.19	0.43	0.46
Wait frequency	−0.36	0.01	−0.39	−0.04	0.37	0.07	−0.21	−0.38	0.18	−0.56	0.26

significantly compared with both age 1 (PERMANOVA, F = 5.71, $p < 0.001$) and age 2 (PERMANOVA, F = 3.95, $p = 0.008$), and in this stage, we observed neither food sharing nor restrain, unlike in earlier age categories. The first component was strongly associated with rejection, carrying duration, breaking contact, leaving, and carrying frequency. This component represents a clear behavioral syndrome of active independence promotion through withdrawal of physical support. The second component was defined by waiting frequency, bridging, waiting duration, and carrying frequency, representing different modes of providing support—either through active assistance or patient supervision. The third component was associated with making contact, waiting duration, and carrying frequency, suggesting variation in who initiates physical contact during this developmental stage.

Bootstrap-Validated Maternal Care Styles by Infant Age

Age 1 (0–3 months)

Bootstrap validation of cluster analysis revealed three stable behavioral strategies during early infancy (Rand Index = 0.71, 95% confidence interval [CI] = 0.43–1), with Jaccard similarity values of 0.83, 0.86, and 0.79. PERMANOVA confirmed that these clusters differed significantly in their behavioral compositions (F = 7.21, $R^2 = 0.69$, $p < 0.001$). Cluster 1 ($n = 9$) is a *Minimal-investment* style, with low scores for all behaviors (Fig. 1). This energy-conserving approach was adopted by most mothers observed during early infancy. Cluster 2 ($n = 1$) is a *Proximity-focused* style, with very high scores on approach coupled with low scores on other behaviors. This mother maintained close spatial monitoring without providing extensive physical support. Cluster 3 ($n = 4$) is a *High-investment* style characterized by high

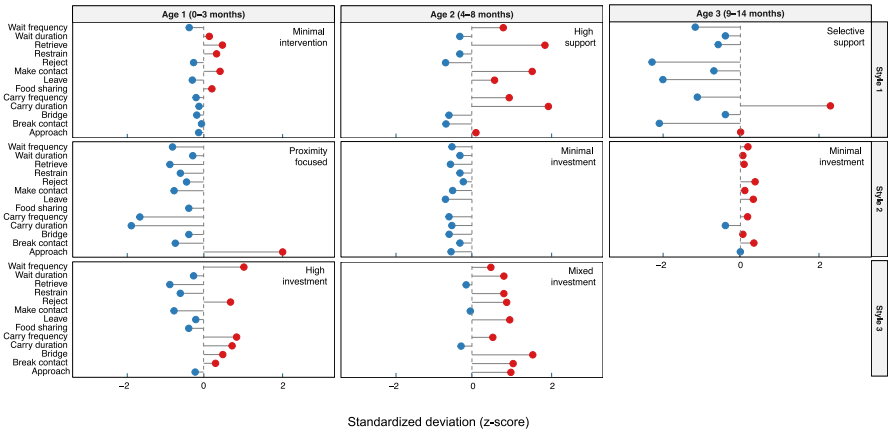

Fig. 1 Behavioral loadings (standardized x-scores) for maternal care styles across three infant age categories in mantled howler monkeys at Los Tuxtlas from September 2021 to September 2023. Each panel represents a distinct maternal style observed during a.

scores in both supportive behaviors (e.g., carry frequency, wait frequency) and limiting behaviors (rejection), suggesting active management of infant behavior.

specific infant age. Red circles show positive loadings (above-average behavior frequency), and blue circles show negative loadings (below-average frequency).

Age 2 (4–8 months)

Bootstrap validation identified three stable behavioral clusters during middle infancy (Rand Index = 0.93, 95% CI = 0.66–1, Jaccard similarities: 0.78, 0.81, and 0.77). PERMANOVA confirmed significant behavioral differences between clusters ($F = 8.54$, $R^2 = 0.63$, $p < 0.001$). Cluster 1 ($n = 2$) is a *High-support* style with elevated caring behaviors (retrieving, carry duration, make contact) and low rejection (Fig. 1). This style provides extensive physical support as infants become more mobile. Cluster 2 ($n = 6$) is a *Minimal-investment* style with consistently low scores across all behaviors, suggesting continued energy conservation. Cluster 3 ($n = 3$) is a *Mixed-investment* style, with high scores on both supportive and limiting behaviors, indicating mothers who actively manage infant independence development.

Age 3 (9–14 months)

Bootstrap validation identified two stable behavioral clusters during late infancy (Rand Index = 0.80, 95% CI = 0.51–1, Jaccard similarities: 0.84 and 0.80). PERMANOVA showed significant differences between these clusters ($F = 10.27$, $R^2 = 0.71$, $p = 0.003$). Cluster 1 ($n = 1$) is a *Selective-support* style with low scores on most behaviors but high carrying duration (Fig. 1), suggesting focused investment in specific contexts. Cluster 2 ($n = 6$) is a *Minimal-investment* style, with low scores on all behaviors, indicating that most mothers converge on low-investment approaches as infants approach independence.

Consistency in Maternal Care Styles Across Infant Development

We observed 11 mothers in at least two developmental periods. This included mothers tracked across consecutive ages and in non-consecutive periods, with six mothers contributing data to all three age comparisons. Pairwise agreement analyses showed minimal style consistency (Figure 2): age 1 to 2 transitions showed very low agreement ($n = 9$, $\kappa = 0.07$, $p = 0.72$), age 2 to 3 transitions showed agreement worse than expected by chance ($n = 7$, $\kappa = -0.20$, $p = 0.15$), and age 1 to 3 transitions showed chance-level agreement ($n = 6$, $\kappa = 0.00$, $p = 1.00$).

PERMANOVA on combined principal component scores from all ages showed that infant age had a highly significant effect on maternal behavioral patterns, explaining 37.9% of the variance ($F_{2,29} = 8.85$, $R^2 = 0.38$, $p = 0.001$). In contrast, maternal identity explained 30.1% of the variance but this effect was not statistically significant when controlling for infant age ($F_{10,21} = 0.90$, $R^2 = 0.30$, $p = 0.437$).

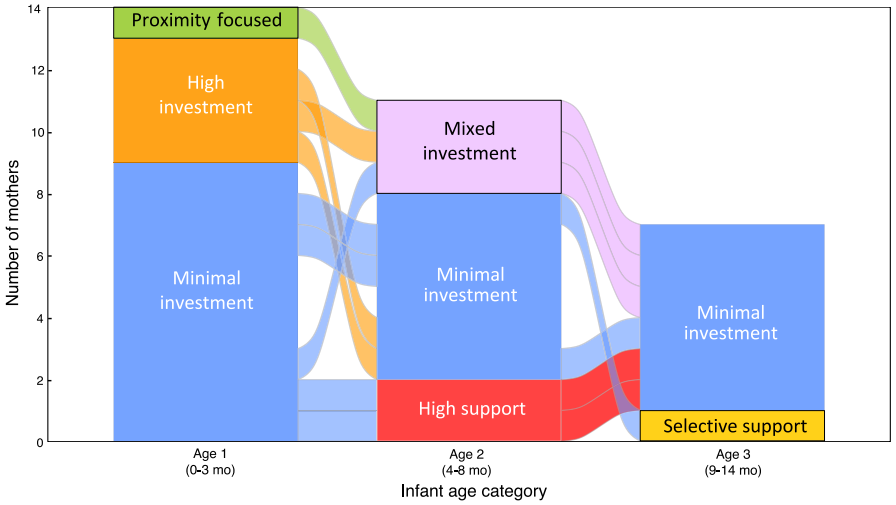

Fig. 2 Maternal care styles per infant age category and style transitions across infant development in mantled howler females studied at Los Tuxtlas (Mexico) from September 2021 to September 2023.

Discussion

We found three key results in our study of maternal care styles in wild mantled howler monkeys: (1) there are distinct maternal care styles at each infant age, with three styles during early infancy (*Minimal-investment*, *Proximity-focused*, and *High-investment*), three during middle infancy (*High-support*, *Minimal-investment*, and *Mixed-investment*), and two during late infancy (*Minimal-investment* and *Selective-support*); (2) individual mothers showed very low consistency in their styles across infant development stages; and (3) infant age was the primary driver of maternal behavioral variation rather than maternal identity. Data collection was severely limited by the challenge of observing medium sized primates over 20 m high in dense tropical forest, resulting in sparse, developmentally unbalanced data that should be interpreted cautiously. Nevertheless, our findings suggest that mantled howler monkey mothers adjust their care strategies in response to the developmental needs of infants rather than maintaining consistent individual styles.

The identification of distinct maternal care styles at each infant age extends our understanding of maternal behavior organization in platyrrhines. The age-specific analytical approach revealed that maternal behaviors cluster into coherent styles, and these styles differ in composition across development stages. During early infancy, the predominance of the *Minimum-intervention* style (9 of 14 mothers) suggests that most mothers adopt a relatively hands-off approach even with very young infants, contrasting with the more protective styles commonly reported in cercopithecines during this period (Bardi & Huffman, 2002; Maestripieri, 1998; Schino et al., 1995). The emergence of a distinct *High-support* style only in middle and late infancy, when infants are becoming more mobile and face greater risks navigating the arboreal environment, suggests that mantled howler mothers strategically increase

protective behaviors during periods of heightened vulnerability rather than maintaining consistently high protection throughout development. However, our interpretation of late infancy patterns must be cautious given the small sample size during this period. Future studies should prioritize equal sampling across all developmental stages to confirm whether the reduction to only two maternal styles in late infancy represents a real developmental pattern or results from limited statistical power.

The reduced consistency in individual maternal styles across infant development contrasts with patterns reported in cercopithecines. Studies of rhesus macaques (Berman, 1980; Maestripieri, 1994) and vervet monkeys (Fairbanks, 1996; Fairbanks & McGuire, 1987, 1988) have emphasized the stability of maternal styles both within and across offspring. However, these studies were conducted in captive or provisioned populations where environmental conditions remain relatively stable. Our wild population faces multiple environmental challenges (e.g., fluctuation in food availability and intraspecific competition: Ceccarelli et al., 2019; Maya-Lastra et al., 2025) and the demands of arboreal locomotion, which may favor behavioral flexibility over consistency. Additionally, few studies have explicitly compared maternal styles across different infant ages as we have done here, making direct comparisons challenging. The apparent variation in mantled howler maternal behavior, however, converges with observations in capuchin monkeys (Verderane & Izar, 2019), Japanese and rhesus macaques (Bardi et al., 2001), and chimpanzees and bonobos (De Lathouwers & Van Elsacker, 2004), suggesting that maternal care styles are more flexible than previously assumed (Berman, 1980 ; Fairbanks, 1996). Nevertheless, our ability to track individual consistency was constrained by observing only six mothers across all three developmental stages. Future longitudinal studies of mantled howler monkeys and other primate species should aim to follow complete cohorts of mothers throughout infant development to establish whether behavioral flexibility is a species characteristic or whether some individuals maintain consistent styles that our limited sampling failed to detect.

Our finding that infant age explains more behavioral variance than maternal identity supports the hypothesis that mantled howler mothers adjust their behavior primarily in response to infant developmental needs. This pattern of increasing independence with age reflects fundamental patterns of primate maternal behavior (Hinde & Spencer-Booth, 1968, 1971). Our results go beyond confirming this general trajectory by showing that the organization of maternal behaviors into distinct styles occurs systematically across development, with specific behavioral combinations emerging and disappearing as infants mature. This systematic reorganization of maternal behaviors across development parallels findings in other primates. For instance, in Assamese macaques (*M. assamensis*), there are distinct behavioral transitions at 2 to 3 months (shifts in proximity maintenance responsibility) and 7 to 8 months (onset of rejection; Arbaiza-Bayona et al., 2025), while Sumatran orangutan (*Pongo abelii*) mothers show individual-specific trajectories in how they adjust carrying and proximity behaviors across offspring development (Revathe et al., 2024). These convergent findings across distantly related primate taxa suggest that age-specific maternal behavioral reorganization may be a fundamental feature of primate maternal care, although the specific timing and patterns vary with species-typical life history traits.

The behavioral flexibility observed in mantled howler mothers likely reflects multiple selective pressures operating in their natural environment. The arboreal habitat presents challenges, with the three-dimensional complexity of the forest canopy requiring developing infants to master complex locomotor skills while facing fall risks (Baldwin & Baldwin, 1973) and shapes both carrying strategies and mother-infant coordination (Nakamichi & Yamada, 2009; Ross, 2001). This may explain why bridging was more frequent during middle infancy when infants are increasingly independent during locomotion. Environmental unpredictability, including seasonal resource variation and predation pressure absent in captive cercopithecine studies, may further select for flexible maternal strategies. Social system differences provide another explanatory dimension: the smaller, cohesive groups of howler monkeys (Di Fiore & Campbell, 2007) contrast with the larger matrilineal societies of many cercopithecines (Kappeler & van Schaik, 2002; Strier, 1994), potentially reducing social pressures that might otherwise stabilize individual behavioral phenotypes. The predominance of *Minimal-investment* style across all ages could also reflect energetic constraints in frugivorous-folivorous primates (Milton, 1996), where mothers must balance infant care with their own metabolic needs. Similar relaxed maternal styles in other arboreal species like Yunnan snub-nosed monkeys (*Rhinopithecus biet*, Li et al., 2013) suggest convergent adaptations to comparable ecological pressures. Future research incorporating physiological measures (Dias et al., 2018; Maestripieri et al., 2009) and examining the influence of infant characteristics (e.g., sex: de la Torre *et al.*, 2021), ecological conditions (e.g., food availability: Revathe et al., 2024), maternal physical condition (Dias et al., 2018), and demographic factors (e.g., group composition: Clarke et al., 1998), could clarify whether style transitions reflect active maternal strategies or passive responses to changing environmental challenges.

In summary, we found that the maternal care of wild mantled howler monkeys is a dynamic system in which mothers adjust their behavioral strategies in response to infant developmental needs rather than maintaining consistent individual styles. The quantitative framework for analyzing age-specific maternal styles that we used provides a foundation for future comparative studies examining how ecological pressures, social systems, and life history strategies shape maternal care across primates.

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Declarations

Inclusion and Diversity The author list includes contributors from the country where the research was conducted, who participated in study conception, study design, data collection, analysis, and/or interpretation of the findings.

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