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BRIEF COMMUNICATION

Infant Handling in Mantled Howler Monkeys

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ABSTRACT

Objectives: In most primate species that live in social groups, non-mothers frequently interact with infants leading to significant impacts on maternal care strategies and both infant socialization and survivorship. In this study, we focused on infant handling by non-mother individuals in mantled howler monkeys (*Alouatta palliata*), a species for which very little information is available on this topic.

Materials and Methods: Using focal-animal sampling for 743 h, we observed 218 instances of interest and 232 handling events involving 14 infants (i.e., 1 to 12 months of age) living in four groups in southern Mexico.

Results: Interest and handling occurred at similar rates, 0.3 events per hour. Most handling was positive, involving behaviors such as making contact and friendly touching, whereas aggressive behaviors, such as harassing and kidnapping, were infrequent. Adult females, especially when lactating, were the primary handlers, contrasting with findings in other primate species where juveniles or non-lactating females are usually more involved. Handling began within the first week of life and was most frequent during the first 3 months. Mothers rarely intervened in handling, doing so primarily during infrequent kidnapping events.

Discussion: These findings contribute to our understanding of primate social behavior, particularly in species with low social activity levels, and provide a basis for future research on the implications of infant handling for group dynamics and infant development.

1 | Introduction

In most primate species mothers typically are the primary caretakers of their offspring. However, attraction to infants often prompts non-mothers to engage with them (Dunayer and Berman 2018). Infant handling encompasses any interactions between infants and non-mother individuals. These interactions may range from curiosity or interest to harassment or alloparenting (Dunayer and Berman 2018; Mitani and Watts 1997; Ross and MacLarnon 2000; Rosenbaum and Gettler 2018; Small 1990). Consequently, infant handling may impact maternal care through either support that improves infant survival, or by potentially endangering infants through physical injury or death (Dunayer and Berman 2018; Silk 1999).

Positive infant handling can be very brief, including touching, nuzzling, or grooming, but it can also span long periods, especially among species in which alloparenting involves carrying (Dunayer and Berman 2017). Conversely, negative forms of infant handling, such as harassment involving fighting, biting, sitting on, or even kidnapping, also exist (Maestripieri 1993; Nicolson 1987). Caretaking or alloparenting can be categorized into direct care activities, that is, feeding, transporting, and maintaining hygiene, and indirect care, such as protection or vigilance (Rosenbaum and Gettler 2018). Positive handling benefits infants, mothers, and handlers (Mitani and Watts 1997; Ross and MacLarnon 2000; Small 1990; Stanford 1992; Xi et al. 2008). For infants, it aids in developing social skills crucial for group living (McKenna 1979; Small 1990). For handlers, it can promote

learning and skill practice, and, indirectly, may improve social status in a dominance hierarchy (Cheney 1978; Hrdy 1976; Silk 1999). For mothers, infant handling by others may benefit them either directly, by allowing them to allocate more time to foraging (Stanford 1992) or grooming (Xi et al. 2008), or indirectly by favoring earlier weaning and thus positively impacting reproductive rates (Ross and MacLarnon 2000).

Handling typically begins during the first weeks or months of life and diminishes as infants mature (Dunayer and Berman 2018; Maestripieri 1993, 1994). The sex and age of handlers vary depending on the species, social bonds, and kin structure of groups. Not all individuals have access to infants: typically, females, and especially juvenile females, are the primary handlers (Kleindorfer and Wasser 2004; Maestripieri 1993, 1994), but males, even when they are not the fathers, may also engage in infant handling (Stead et al. 2021; Wright 1990). Relatives typically have greater access to infants compared to non-relatives. For example, in mountain gorillas (*Gorilla beringei beringei*), a species in which females typically disperse from natal groups, resulting in weak social bonds among females, mothers tend to be more reluctant to allow handling by non-related individuals (Grueter et al. 2019). Furthermore, yellow baboon infants (*Papio cynocephalus*) usually receive positive handling by relatives but negative handling by non-relatives (Kleindorfer and Wasser 2004). Relatives can act as helpers, allowing mothers to benefit from time away from infants for foraging, self-care, or social interactions (Mitani and Watts 1997; Ross and MacLarnon 2000; Xi et al. 2008). In some species, "marketplace" dynamics are observed where handlers groom mothers in exchange for access to infants (Henzi and Barrett 2002; Fruteau et al. 2011). Rank tends to have different effects on handling depending on the species. For instance, in yellow baboons and rhesus macaques (*Macaca mulatta*), the infants of high-ranking mothers are handled more frequently than those of low-ranking females (Cheney 1978; Dunayer and Berman 2017). However, in bonnet macaques (*Macaca radiata*) handling is directed downward in the hierarchy, with low-ranking infants being handled more than high-ranking infants (Silk 1999).

Howler monkeys (*Alouatta*) are arboreal platyrrhines that produce one infant at a time, have non-seasonal reproduction, and have a mean interbirth interval of approximately 25 months (Cristóbal-Azkarate et al. 2017; Dias et al. 2023). The activity budget of howler monkeys is heavily skewed toward resting, with socialization accounting for less than 2% of their daily activities (Crockett and Eisenberg 1987; Di Fiore and Campbell 2007). While various aspects of their social interactions, foraging habits, ontogeny, life history, and physiology have been extensively studied, there remains a notable gap in our understanding of infant handling in howler monkeys. Infant handling has been described in two species of howler monkeys, black-and-gold howler monkeys (*A. caraya*; Calegaro-Marques and Bicca-Marques 1993) and mantled howler monkeys (*Alouatta palliata*; Clarke 1990; Clarke, Glander, and Zucker 1998). Similarly to other primates, offspring handling in howler monkeys is more frequent during early infancy (Calegaro-Marques and Bicca-Marques 1993; Clarke 1990; Clarke, Glander, and Zucker 1998). Affiliative behaviors, such as carrying or bridging, have been observed, along with instances of kidnapping and some harassment. Additionally, all age-sex classes perform various forms of offspring handling. Mantled howler monkey handlers direct more negative and harmful interactions to infants than black-and-gold howler monkeys, and in the former, harmful interactions are directed down the female dominance hierarchy (Clarke, Glander, and Zucker 1998). In black-and-gold howler monkeys, adult females exhibit more allomaternal behavior than other sex-age classes (Calegaro-Marques and Bicca-Marques 1993; Clarke 1990; Clarke, Glander, and Zucker 1998). Males do not actively participate in infant care but generally tolerate the presence of infants and occasionally interact with them (Bolin 1981; Calegaro-Marques and Bicca-Marques 1993; Clarke 1990; Clarke, Glander, and Zucker 1998).

In this study, we examined infant handling in previously unstudied groups of mantled howler monkeys to further our understanding of variation in this behavior. We describe the types of behaviors displayed by infants, handlers, and mothers, as well as the age and sex of actors. Additionally, we hypothesized that the likelihood of observing infant handling varies with infant age and that handling varies across age-sex classes. Specifically, we expected that handling would decrease with increasing infant age and that adult females and immatures would be the most frequent handlers.

2 | Methods

2.1 | Ethical Note

We complied with the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates and with the Code for Best Practices in 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.

2.2 | Study Site

The study was conducted at Los Tuxtlas (18°37′–18°35′ N, 95°08′–95°05′ W), located in southeast Veracruz, Mexico. This region comprises several types of vegetation, including mangroves, low deciduous rainforests, high evergreen rainforests, mid sub-evergreen rainforests, mesophyll mountain forests, and pine forests (Vázquez-Torres et al. 2010). Annual rainfall varies between 1500 and 4500 mm and mean ambient temperatures range between 22°C and 26°C. There is a rainy season from June to December, with abundant rains and thunderstorms, and a dry season from January to May. Northern winds occur during autumn and winter, producing rainstorms and a decrease in ambient temperature (Soto and Gama 1997). We observed four groups of mantled howler monkeys in three forest fragments (Table 1).

2.3 | Study Subjects

We identified all subjects by their physical characteristics. We determined infant age through the observation of births and anatomical features such as fur color and size (Balcells and Veà 2009). We focused on the 14 infants of up to 1 year of age, that is, non-weaned (Balcells and Veà 2009), living in four

TABLE 1 | Attributes of study sites and mantled howler monkey groups.

	Site/group			
	La Flor de Catemaco		Balzapote	Cerro del Borrego
Attribute	**Group 1**	**Group 2**	**Group 3**	**Group 4**
Group location	18°26′18″ N 95°03′12″ W	18°26′41″ N 95°03′04″ W	18°36′38″ N 95°04′11″ W	18°38′32″ N 95°05′30″ W
Habitat size (ha)	100	100	8	78
Number of groups in site	4	4	2	2
Group size	15–19	10	8–12	23
Number females	4–6	5	4	8
Number of males	3–4	4	2–3	10
Number of juveniles	8–11	0	1–2	3
Number of infants	2–4	1	2–5	2–4

groups (Table 2). We classified handlers as adults (either females or males) or immatures (i.e., infants, juveniles, or subadults). Given that sex cannot be visually determined in immature individuals of this species (Clarke et al. 2007), we could not assess whether immature handlers were female or male.

2.4 | Behavioral Sampling

From September 2021 to September 2023, we followed study groups for 8 h per day, during which we used the focal-animal sampling method with a continuous recording technique to observe infants for up to approximately 7 h. In each focal sample we recorded all instances of infant interactions with non-mother group members (Table 3). These ranged from interest (i.e., looking at the infant) to affiliative (e.g., friendly contact) and agonistic interactions (e.g., harassing). Each time an interaction with a non-mother occurred, we recorded its duration, the identity of the actor, the identity of the non-mother individual, and the behavior of the mother. Playing among immatures was not considered in this study. We stopped focal samples when infants were out of sight and resumed them when they became visible. If infants were out of sight for longer than 1 h, another focal subject was followed for the remainder of the day. We collected 743 h of focal observations over 77 days.

2.5 | Data Organization and Analysis

Given the small sample of groups, infants, and behaviors that we studied per infant age, our results are primarily descriptive. Specifically, we describe our results using rates of behaviors and percentages of observations. We divided the results section into two parts, one dedicated to "interest", the only act that did not involve physical contact between infants and handlers, and another focused on all other behaviors. In each of these parts, we indicate the ages of the infants and the sex and age class of handlers. For handling, we also describe the incidence of positive and negative behaviors. We used chi-square tests to examine if variation in interest and handling was influenced by infant age in months (with expected frequencies weighted by observation effort per infant age) and by the age and sex class of handlers (i.e., adult female, adult male, immature, with expected frequencies weighted by the number of individuals in each class).

3 | Results

We recorded 218 cases of interest in infants, corresponding to a rate of 0.3 events per hour (0.02 events/h/infant). The youngest individual to receive interest was 2 days old and the oldest was 8 months, although 89% of interest events occurred during the first 3 months of infant age ($\chi^2_3 = 1019.8.6$, $p < 0.001$; Tables S1 and 4). Adult females were the primary non-mothers interested in infants (57% of the events), especially when they were lactating (43%), followed by immatures (24%), and mature males (19%; $\chi^2_3 = 116.6$, $p < 0.001$; Tables S1 and Table 4). During interest events mothers stayed mostly inactive (95% of the events) but rejected the non-mother in 5% of the events. Only 21% of interest events were followed by infant handling.

There were 232 infant handling events (0.3 events/infant, 0.02 events/h/infant; Table 2). Handling occurred between infant ages 3 days and 12 months, but most (70%) happened during the first 3 months of life ($\chi^2_{12} = 29.5$, $p < 0.001$; Table S2). Positive handling occurred in 82% of the events and only 3% led to kidnapping (Table 4). Handling events lasted around 1 min, with harassment and kidnapping having the shortest and longest durations, respectively (Table 4). Positive handling was more frequent and observed until older infant ages (Figure 1A) than negative handling, which was more frequent at early ages (Figure 1B). Making contact and friendly contact were the most frequently observed behaviors and occurred in almost all infant ages. Kidnapping was the least frequently observed behavior, although it was associated with the disappearance of an infant.

Adult females were the primary nonmother individuals to interact with infants with 59% of the events (and in 75% of those events females were lactating), followed by adult males (24%), and immatures (16%; $\chi^2_3 = 144.8$, $p < 0.001$; Tables S2 and 4).

TABLE 2 | The number of infant handling events per group and subject according to infant age.

		Infant age (months)												
Group	**Subject**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**Total**
Group 1	H1C1	NA	1 (0.8)	1 (9.9)	NA	NA	NA	NA	NA	NA	NA	NA	NA	2 (10.8)
Españolas	HAC1	10 (10.8)	22 (16.6)	3 (18.1)	NA	1 (6.8)	NA	NA	0 (21.3)	1 (19.9)	0 (8.5)	0 (5.0)	NA	37 (106.8)
Españolas	HAC2	7 (14.8)	1 (8.0)	0 (6.5)	NA	NA	NA	NA	NA	NA	NA	NA	NA	8 (29.3)
Españolas	HPGC1	NA	10 (15.4)	7 (10.2)	9 (17.3)	0 (4.8)	0 (6.8)	NA	NA	1 (14.1)	1 (12.5)	0 (6.6)	0 (5.2)	28 (92.7)
Españolas	HPMC2	1 (0.08)	17 (14.5)	7 (16.2)	2 (6.2)	NA	0 (7.6)	NA	1 (4.0)	0 (15.3)	1 (14.6)	0 (10.9)	0 (7.7)	29 (97.2)
B2	HB1C1	NA	NA	NA	NA	NA	0 (4.0)	NA	0 (7.4)	1 (7.2)	1 (7.5)	3 (6.2)	NA	5 (32.3)
B2	HB1C3	4 (14.2)	8 (27.8)	0 (9.1)	2 (7.0)	1 (7.0)	1 (14.1)	NA	NA	NA	NA	NA	NA	16 (79.2)
B2	HB2C1	NA	NA	6 (6.8)	2 (7.2)	0 (7.2)	2 (15.6)	NA	NA	NA	1 (12.7)	NA	3 (12.7)	14 (62.2)
B2	HB2C2	1 (13.8)	0 (6.7)	0 (19.5)	2 (13.7)	5 (7.1)	3 (5.1)	NA	NA	NA	NA	NA	NA	11 (65.8)
B2	HB3C1	6 (14.75)	1 (7.7)	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	7 (22.4)
B2	HB3C2	3 (12.1)	16 (13.7)	2 (0.08)	NA	NA	NA	NA	NA	NA	NA	NA	NA	21 (25.8)
B2	HB4C1	0 (7.7)	6 (5.8)	19 (12.8)	2 (11.6)	NA	NA	5 (13.3)	10 (7.2)	5 (6.8)	1 (13.2)	0 (7.0)	0 (6.2)	48 (91.4)
Cerro del Borrego	HCDB1C1	4 (14.3)	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	4 (14.3)
Cerro del Borrego	HCDB2C1	NA	NA	NA	NA	NA	2 (9.4)	0 (3.3)	NA	NA	NA	NA	NA	2 (12.7)
Total		36 (102.4)	81 (116.9)	46 (109.3)	19 (62.9)	7 (32.9)	8 (62.6)	5 (16.6)	11 (39.8)	8 (63.2)	5 (69.0)	3 (35.7)	3 (31.8)	232 (743)

Note: NA indicates that the subject was not sampled at that age. Numbers in parenthesis are the number of sampling hours.

TABLE 3 | Behavioral interactions associated with infant handling in mantled howler monkeys.

Interaction	Description	Actor	Outcome[a]
Attempt	The non-mother initiates any of the interactions described below with the infant but stops due to the intervention of the mother	Non-mother	Variable
Friendly contact	Touching, grooming, embracing, playing	Non-mother	Positive
Harassing	Negative behaviors like rough grabbing, pulling, dragging, and direct aggression (e.g., slap, bite)	Non-mother	Negative
Interest	Looking at the infant while being in proximity (< 5 m)	Non-mother	Neutral
Kidnapping	Prevent an infant from returning to its mother, by retreating from the mother while carrying the infant	Non-mother	Negative
Taking	Taking the infant from its mother	Non-mother	Negative
Making contact	The infant contacts a non-mother while away from its mother	Infant	—
Transferring	The infant goes from its mother directly to a non-mother	Infant	—
Following	The mother follows the non-mother as it moved with the infant	Mother	—
Rejection	The mother prevents the infant from being taken by the non-mother (via pushing or moving away)	Mother	—
Restraining	Preventing the infant or the non-mother (while carrying the infant) from breaking contact or leaving	Mother	—
Retrieving	The mother actively picks up her infant	Mother	—

[a]Scale refers to the immediate consequences to the infant of interactions initiated by non-mothers, which could be positive, neutral, or negative. As the category "attempt" could be associated with any of the non-mother behaviors, its scale could be positive, neutral, or negative.

Infants were actors in 47% of the events (Figure 2). Mothers did not show any response (i.e., follow, reject, restrain, or retrieve) in most handling events (87%) although they displayed a behavioral response in 100% of kidnapping events and 80% of attempt events; they reacted in only 1% of transfers (Figure 3A). Mothers responded to 14% of the events in which the handler was a female, followed by 13% when they were immature, and 10% when they were male (Figure 3B).

4 | Discussion

In this study we examined infant handling patterns in mantled howler monkeys. We found that both interest in and handling of infants decreased with increasing infant age. Adult females were the most frequent handlers, and handling behaviors were predominantly positive. Mothers rarely intervened, except in cases of negative behaviors, such as kidnapping. Thus, we provide novel insights into the patterns of infant handling in mantled howler monkeys, a topic that has been understudied in this species.

Non-mothers' interest in infants is likely motivated by their physical appearance (Dunayer and Berman 2018), with non-mothers showing interest in infants primarily during the first 3 months and persisting until month 8. This differs from a previous report for a different site, Hacienda La Pacifica (Costa Rica), where interest persisted until month 20 (Clarke 1990). Possible reasons for this discrepancy include social and environmental differences, such as variation in group size, habitat quality, and climatic factors, which could influence social dynamics by affecting resource availability, seasonal foraging demands, and stress levels (Emery Thompson 2017). In larger groups and habitats with abundant resources or favorable climatic conditions, adults may have more opportunities to engage in social interactions, potentially prolonging non-maternal interest in infants. However, adult group sizes were similar in our study and Clarke's (1990) and Los Tuxtlas is a more productive habitat compared to Hacienda La Pacifica, as proxied by rainfall (2600–4500 mm vs. 900–2400 mm of annual rainfall; Janzen 1986; Soto and Gama 1997), so future research could focus on examining how such environmental productivity influences the duration and nature of infant-directed behaviors in different populations.

The handling observed here does not represent true alloparenting due to the absence of care activities, such as carrying. Although adult females, especially lactating females, were the primary handlers, and adult males participated in 24% of events, neither exhibited behaviors indicative of care, except for one instance of protective hugging by a female during rain. These results contrast with reports of alloparental care in black howler (*Alouatta pigra*) and black and gold (*Alouatta caraya*) howler monkeys, where both females and males provide care (e.g., by carrying infants; Bolin 1981; Calegaro-Marques and Bicca-Marques 1993).

The recorded rates of handling behavior are low compared to other primates, such as captive vervet monkeys (*Chlorocebus pygerythrus*, 19 events/h; Fairbanks 1990) and both wild Japanese (*Macaca fuscata*) and captive bonnet macaques (5 events/h; Sekizawa and Kutsukake 2022; Silk 1999), but these rates were higher than those observed in mountain gorillas (0.05 events/h; Grueter et al. 2019). Within mantled howler monkeys, these

TABLE 4 | Duration (in min) and frequency of infant handling interactions according to age-sex of handler and infant age (in months) in mantled howler monkeys.

		Non-mother			
Interaction	**Measure**	**Female**	**Male**	**Immature**	**Total**
Attempt	Total duration	0.73	0.12	0.20	1.05
	Mean duration	0.37	0.12	0.10	0.21
	Frequency	2	1	2	5
	Infant ages	1	3	1–3	1–3
Friendly contact	Total duration	46	16	7.5	69.5
	Mean duration	1	0.73	0.52	0.85
	Frequency	45	22	14	81
	Infant ages	1–12	1–10	1–5	1–12
Harassing	Total duration	7	2.2	3	12.2
	Mean duration	0.77	0.27	0.73	0.57
	Frequency	9	8	4	21
	Infant ages	1–9	1–6	1–2	1–9
Interest	Total duration	44	5.2	1.9	51.1
	Mean duration	1.08	0.55	1.22	0.98
	Frequency	124	42	52	218
	Infant ages	1–3, 8	1–3, 8	1–2	1–3, 8
Kidnapping	Total duration	37.1	2	0	39.1
	Mean duration	17	2	0	6.88
	Frequency	3	1	0	4
	Infant ages	1	2	0	1–2
Making contact	Total duration	47.3	5	5.3	58.6
	Mean duration	1.43	0.35	1.07	1.1
	Frequency	33	14	5	52
	Infant ages	2–12	1–12	2–4	1–12
Taking	Total duration	18.2	0.45	0	18.7
	Mean duration	1.4	0.45	0	1.33
	Frequency	13	1	0	14
	Infant ages	1–3	3	0	1–3
Transferring	Total duration	34	9.3	9	52.3
	Mean duration	1	1	0.7	0.95
	Frequency	33	9	13	55
	Infant ages	1–4	2–3	2–4	1–4

rates also exceeded both affiliative (0.06 events/h) and agonistic (0.03–0.07 events/h) interactions observed among adults (Dias et al. 2010; Ho et al. 2014), suggesting a distinct, potentially important role of infant handling in their social structure. Interestingly, unlike other species where juveniles or sub-adults often interact with infants, adult females maintained the role of primary handlers throughout infant development, and handling behaviors remained largely positive, with no injurious behaviors observed (Fairbanks 1990; Schino et al. 2003; Silk 1999).

Kidnappings, although rare, occurred primarily during the first few months of life and involved lactating females of the same group, in contrast to rhesus macaques, where non-lactating females often carry out kidnappings (Maestripieri 1993). Despite

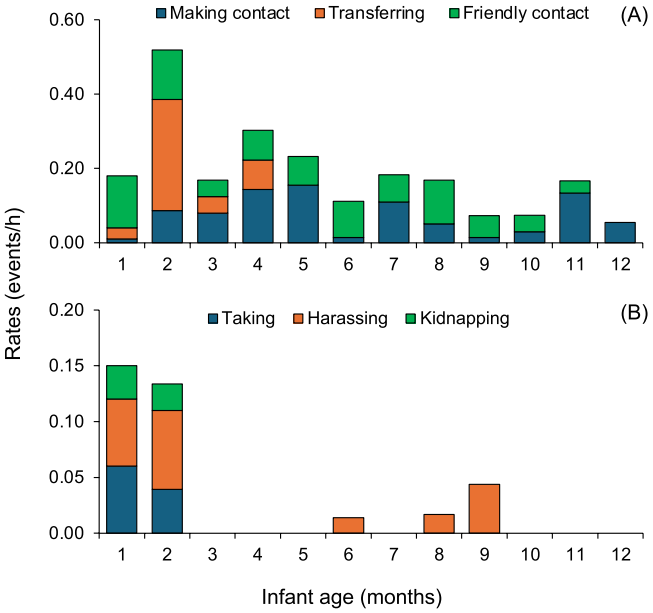

FIGURE 1 | Rates of positive (A) and negative (B) infant handling according to infant age (in months).

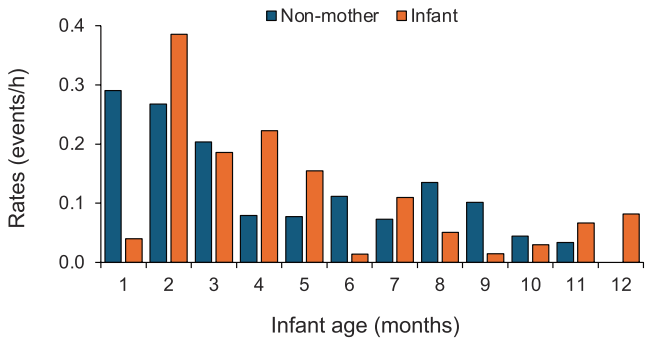

FIGURE 2 | Rates of infant handling according to actor identity (non-mother or infant).

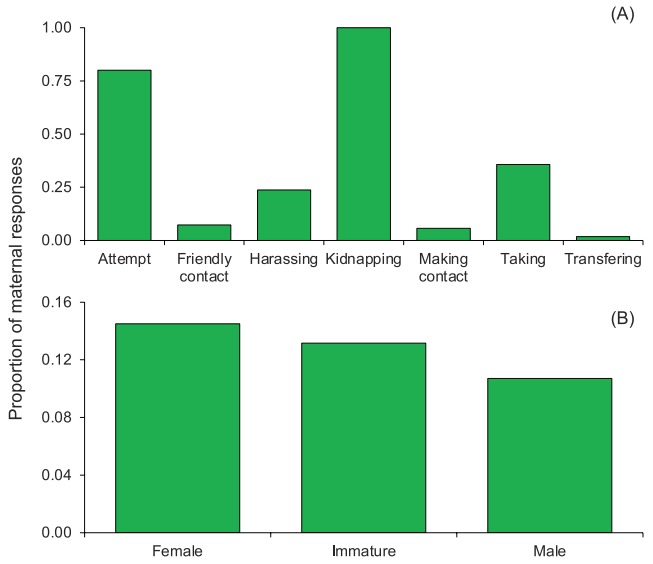

FIGURE 3 | Proportion of maternal responses according to the type of infant handling behavior (A) and the age-sex of handlers (B).

its rarity, the consequences of kidnapping can be severe, as evidenced by one case of prolonged separation resulting in the disappearance of an infant. Maternal intervention in handling events was minimal (11%), typically in response to negative behaviors such as kidnapping, in contrast to rhesus macaques where maternal retrieval accounts for about one-third of handling outcomes (Maestripieri 1993). This reflects a relatively safe social environment for infants, as mothers in mantled howler monkeys did not leave the group but were observed to flee from particularly interested individuals (Clarke, Glander, and Zucker 1998). Although the existence of dominance relationships has not been assessed in this population, the fact that mothers did not leave the group suggests that rank-based relationships, if present, may have a limited influence on infant handling behaviors compared to other populations (Clarke, Glander, and Zucker 1998). Such a safe environment may reduce maternal competition and allow infants more autonomy to explore and engage socially.

Both males and females participated equally in harassment behaviors, hinting at complex social dynamics. Unlike black howler monkey males, however, mantled howler monkey males did not display affiliative behaviors toward infants (Bolin 1981). These differences suggest species-specific social structures and underscore the need for further research to understand the role of kinship and social bonds in infant handling (Stead et al. 2021).

Overall, this study provides valuable data on the social dynamics of mantled howler monkeys and shows significant differences from previous studies, including higher tolerance and lower aggression toward infants. There was a greater degree of interaction between infants and non-maternal females than observed by Baldwin and Baldwin (1973), but no evidence of injury as reported by Clarke (1990) and Clarke, Glander, and Zucker (1998). These findings highlight the importance of further studies to elucidate the effects of infant handling behaviors on the development and social structure of mantled howler monkeys.

Author Contributions

Maud C. M. Czerwinski: conceptualization (equal), data curation (equal), investigation (equal), methodology (equal), visualization (equal), writing – original draft (equal). **Ariadna Rangel-Negrín:** conceptualization (equal), formal analysis (equal), funding acquisition (equal), methodology (equal), project administration (equal), resources (equal), supervision (equal), writing – original draft (equal). **Pedro A. D. Dias:** conceptualization (equal), data curation (equal), formal analysis (equal), funding acquisition (equal), investigation (equal), methodology (equal), project administration (equal), resources (equal), supervision (equal), validation (equal), visualization (equal), writing – original draft (equal).

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data analyzed in this study are presented in the manuscript and its Supporting Information.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.