

# Leadership and the finder's advantage in mantled howler monkeys

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## Abstract

Leading collective movements and arriving first at feeding sites may improve food acquisition. Specifically, the first individual to discover and exploit a feeding site may gain a feeding advantage known as the “finder's advantage.” The aim of this research was to verify if the probability of leading group movements to feeding sites in mantled howler monkeys (*Alouatta palliata*) varied by sex and reproductive status, and whether finders had higher foraging success than followers. We studied 18 adult individuals from two groups in La Flor de Catemaco over a year (978 h), and sampled group movements ( $n = 211$ ) and foraging behavior ( $n = 215$  feeding episodes). Gestating females were leaders and finders of group movements to feeding sites more often than expected but were also replaced in the leading position more frequently than individuals of other sex/reproductive states. Feeding behavior was not influenced by the order of arrival at feeding sites per se, but gestating females had higher food intake rate, bite rate, and feeding time when arriving earlier (i.e., occupying front group positions) than later. Therefore, leadership and the finder's advantage occur in this species and are probably employed by gestating females to maintain their energetic condition.

## KEYWORDS

*Alouatta*, collective movement, feeding, foraging, gestation

## 1 | INTRODUCTION

Group formation is advantageous for many animal species, providing increased protection against predators, access to food resources, opportunities for reproduction, and information exchange (Boesch, 1996; Hoogland & Sherman, 1976; Jarman, 1974; Pulliam & Caraco, 1984; van Schaik, 1983). Effective coordination of group movements is vital for gregarious animals, especially when determining which resources to access, which paths to follow, and for how long to remain in a certain area (Erhart & Overdorff, 1999; Leca et al., 2003; Tecot & Romine, 2012). Leaders are individuals who hold front positions

during movements and trigger a following behavior in most or all members of their groups, exerting social influence over them based on their rank, experience, social status, or specific behavior (King, 2010; King et al., 2009; Petit & Bon, 2010; Sueur & Petit, 2008). Leaders can significantly influence energy expenditure, food intake, and predation risk of other individuals in their groups, which can have important fitness consequences (Conradt & Roper, 2005). Understanding the dynamics of collective movements is, therefore, essential for predicting the fitness and survival of gregarious animals in natural populations.

In group living mammals, individuals that act first are often those with greater motivation (e.g., chacma baboon, *Papio ursinus*: King

et al., 2008; plains zebra, *Equus burchelli*: Fischhoff et al., 2007). However, motivation to engage in a particular activity at a given time varies among individuals (Conradt & Roper, 2005), so members of the same social group must decide when to follow or ignore their conspecifics (King, 2010; King & Sueur, 2011). If individuals do not reach a consensus, the group may fission, resulting in a potential reduction of the benefits of grouping (Conradt & Roper, 2005; Krause & Ruxton, 2002). Cohesion and synchrony among group members are important for survival, and it is expected that natural selection favors individual behaviors that result in advantageous decisions for most group members (King & Sueur, 2011; Schradin et al., 2012). Diurnal primates are typically group foragers, and thus may potentially benefit from shared information on when, how, and what to eat (Trapanese et al., 2019; Visalberghi & Addessi, 2001). However, foraging in groups can also entail resource competition (Schülke & Ostner, 2012), which highlights the importance of leadership and coordination in collective movements. By understanding the dynamics of leadership in primate groups, and studying the foraging activities of leaders and followers, we can gain insight into the factors that contribute to the survival and reproductive success of primates in natural populations.

Nutritional needs vary between males and females, and among females in different stages of the reproductive cycle (Garber, 1987). Female investment in offspring is typically higher than that of males in most primate species due to the costs of gestation and lactation (Garber, 1987; Key & Ross, 1999; McFarland, 1997). Females can modify foraging behavior in response to their reproductive state and according to their nutritional needs, such as selecting specific food items and altering the amount of time spent foraging to cope with the costs associated with different reproductive stages (e.g., Amato et al., 2014; Bicca-Marques, 2003; Dias et al., 2011; Serio-Silva et al., 1999). They may lead their groups to food resources that meet the energy and nutrient requirements of their reproduction. For instance, white-handed gibbon females (*Hylobates lar*) typically lead group movements and have priority of access to food resources (Barelli et al., 2008). These findings highlight the significance of sex and reproductive state, and associated behaviors, in shaping the dynamics of collective movements in primates. However, the influence of the interaction among female reproductive state, food availability, and behavior on the maintenance of energy balance has been described in only a few species (e.g., Cano-Huertes et al., 2017).

Assuming a leading position during a collective movement can result in feeding benefits. The first individual to discover and exploit a feeding site may gain a feeding advantage known as the “finder's advantage” (Caraco & Giraldea, 1991; De la Fuente et al., 2019; Giraldeau & Caraco, 2018). This advantage pertains to the quantity of resources obtained by the finder (Di Bitetti & Janson, 2001), defined as the finder's share (i.e., the proportion of the food items obtained by the finder: Vickery et al., 1991). Leading a group movement toward a feeding site can enhance foraging efficiency by enabling maximization of the intake of high-nutrient and high-energy foods, which can increase reproductive success (Barelli et al., 2008; Boinski, 1991; Erhart & Overdorff, 1999; Janson, 1990; Robinson, 1981). For females, arriving first at a feeding site can be particularly important, as it may

provide improved access to high quality food items, which are critical for the survival of both mothers and offspring (Emery Thompson, 2013). Finders have a temporal advantage by beginning to exploit feeding sites before followers, which can result in higher food ingestion (Di Bitetti & Janson, 2001). In primates, lactating females adjust feeding behavior to meet energy demands through, for instance, increased feeding time (Altmann, 1980; Dunbar & Dunbar, 1988; Koenig et al., 1997), food quantity (McCabe & Fedigan, 2007; Sauther & Nash, 1987), or food quality (Boinski, 1988; Murray et al., 2009; Sauther, 1994). In this context, leadership and the finder's advantage could be behaviors used by females to maintain their energy balance through the reproductive cycle.

Our study focused on investigating the roles of group leadership and the finder's advantage on the feeding behavior of mantled howler monkeys (*Alouatta palliata*). We have previously reported that in this species females lead and take front positions more often than males during group movements toward feeding sites, particularly during gestation (Ceccarelli et al., 2020). In that study, however, we did not assess either replacement patterns in leadership (i.e., stability, defined as when the same individual initiates and terminates a group movement toward a feeding site) or variation in the feeding behavior of individuals with respect to their position in group movements. The energy balance of female mantled howler monkeys decreases from gestation to lactation and to cycling (Rangel Negrín et al., 2018, 2022), and reproductive females (i.e., gestating and lactating) have higher glucocorticoid and thyroid hormone levels than cycling females and males (Dias et al., 2017). Thus, here we explored how variation in nutritional and energy demands, proxied by sex and reproductive state, impact these behaviors. We tested two hypotheses. First, if arriving first at a feeding tree allows for gaining preferential access to food resources, then individuals will use it based on their energy/nutritional demands, so the probability of acting as leaders of group movements toward feeding sites and finders of feeding sites will vary according to sex and reproductive state. Accordingly, we predicted that gestating and lactating females would have a higher likelihood of (i) initiating group movements toward feeding sites, (ii) being finders of feeding sites, and (iii) having the highest probability of both initiating group movements and finding feeding sites (i.e., not being replaced in front positions) compared to cycling females and males. Second, if the finder's advantage is used to gain preferential access to food resources, foraging patterns should vary among individuals depending on their order of arrival at feeding sites. We thus predicted that individuals arriving early at feeding sites (i.e., finders) should have higher food intake, higher bite rates, and shorter feeding times compared to followers.

## 2 | METHODS

### 2.1 | Study site and subjects

The study was conducted at La Flor de Catemaco (18°26'43" N, 95°02'49" W), an agroforestry ranch located in the Los Tuxtlas

Biosphere Reserve. In this site, the understory is interspersed with palm plantations, but the canopy and emergent strata correspond to tall, evergreen vegetation typical of mature forests (Bongers et al., 1988). The climate is warm and humid, with a monthly average temperature of 27°C, a summer rainfall regime from June to September (Soto, 2004; Soto & Gama, 1997), and a dry season between March and May (Dias & Rodríguez-Luna, 2003). The mean annual rainfall is 2600 mm (Ceccarelli et al., 2020).

For this study, we focused on two groups that have been monitored since 2012 (Dias et al., 2023). Group 1 comprised eight adult individuals, four males and four females; and Group 2 consisted of 10 adults, four males and six females. Immature individuals (i.e., <36 months old) were also present in both groups, but we only collected data from the 18 adults (which were habituated to the presence of researchers and individually identified). We categorized females into one of three reproductive states: gestating, during the 6 months preceding the birth of their offspring (Glander, 1980); lactating, when they had an offspring less than 6 months old, which is the exclusive lactation period (Balcells & Baró, 2009); and cycling, when they were not pregnant or lactating. This classification was based on observations of births during and up to 6 months following the end of the behavioral recording, and, in the case of offspring present at the beginning of the study, on available birth records for the population. According to this classification, during the study period, six females were recorded in three reproductive states, one female was lactating and cycling, one female was lactating and gestating, and two were only recorded as cycling (Supporting Information S1: Table 1). This classification of female reproductive states is consistent with physiological, demographic, and behavioral observations in this species (e.g., Cano-Huertes et al., 2017; Dias et al., 2017; Rangel Negrín et al., 2022). Yet, in the absence of data on the physiological state of females (e.g., hormonal profiles), in this study the cycling stage corresponds to females that were neither gestating nor lactating.

## 2.2 | Behavioral sampling

From October 2020 to October 2021 (978 h of fieldwork), we divided fieldwork into periods of 4 days per group per week and conducted behavioral observations between 7:00 and 16:00. With all occurrences sampling (Altmann, 1974), we observed group movements defined as every time the majority (i.e., >50%) of the adult group members moved to a different tree and engaged in a different activity from that in the starting tree. We focused on the subset of group movements that finished on a feeding site ( $n = 220$ ), defined as a tree where individuals displayed feeding behavior (i.e., inspect food, bring food to mouth, chew, and swallow; Ceccarelli et al., 2020; Rangel Negrín et al., 2022). During this sampling we recorded the identity of the leader (i.e., the individual who moved first toward a feeding site) and the finder (i.e., the individual who arrived first at a feeding site).

We used focal-animal sampling with continuous recording (Altmann, 1974) to study the feeding behavior of mantled howler monkeys. Following a preestablished sequence that aimed at balancing observation effort among individuals, we selected a subject to be sampled once a group movement began. When this subject arrived at a feeding site, we recorded its order of arrival (i.e., 1–8 in Group 1; 1–10 in Group 2) and started the focal sampling. During focal sampling, we recorded the start and end times of feeding, the type of food consumed (i.e., ripe or unripe fruit, mature or young leaves, flowers), and the plant species. We also recorded the number of bites displayed by the focal individual, defining a bite as each occasion the individual introduced food into its mouth during a feeding episode. When subjects did not consume a complete or single food unit (understood as one fruit, leaf, or flower) in one bite, we recorded the proportion of the unit taken into the mouth (e.g., half, one-fourth) or the number of consumed units, respectively (Reynoso-Cruz et al., 2016). We considered a feeding period to end when the focal individual did not display feeding behaviors for >5 min (Vogel & Janson, 2007). We recorded the duration of periods in which the focal individual could not be observed. When the focal individual finished feeding, we sampled the next scheduled individual once a group movement began. We performed a total of 220 focal animal samples: 68 for cycling females; 45 for gestating females; 20 for lactating females; 87 for males. We could not collect complete information on subject behavior (e.g., we could not determine the food item that was consumed) in three focal samples, which were thus excluded from analysis (Supporting Information S1: Table 2).

## 2.3 | Measures of feeding behavior

Following feeding episodes, we collected 10 units of the food items consumed by focal individuals from the same trees where feeding occurred. When individuals used the same food item from the same tree species in consecutive feeding episodes (24% of the feeding episodes) we only collected food items from the first used tree. For 6% of the feeding episodes, we could not collect the food items used by mantled howler monkeys because they were inaccessible.

We weighed the mass of the 10 units and dried them in a Nesco dehydrator (American Harvest FD-80) at <60°C on the same day of sample collection. We weighed (to the nearest 0.001 g) each 10-unit sample during drying and considered samples to be dried when they had the same weight in three consecutive measurements, taken 8 h apart. We then weighed each food unit and calculated the mean unit weight across all units from the same item/species/feeding episode sample.

We calculated three feeding behavior measures per feeding episode: feeding time; bite rate; and food intake rate. We calculated feeding time as the time elapsed between the beginning and the end of each feeding episode (in min) and bite rate as the number of bites divided by feeding time per feeding episode (bites/min). To calculate the food intake rate, we first multiplied the mean weight (in g) of

consumed food units per the number of units consumed per food bite. We then multiplied this result by the number of food bites taken per feeding episode and divided the result by the duration of the feeding episode.

## 2.4 | Data organization and analysis

To test the predictions of the first hypothesis (i.e., differences in the likelihood of leading, finding, and leadership replacement during movements toward feeding sites dependent on sex/reproductive state) we used  $\chi^2$  analysis to assess deviations from expected values. In these tests, we tallied expected frequencies by the number of times each individual could have acted as either leader (i.e., began a group movement toward a feeding site) or finder (i.e., was the first to arrive at a feeding site) given the total number of group members in each sex/reproductive state. Leadership replacement was defined as each occasion in which the individual who began a group movement toward a feeding site was replaced by another individual in the front position. We had complete information on the identity of the leader, finder, and replacements for 211 movements.

To test the predictions of the second hypothesis we ran three LMMs, in which food intake, bite rate, and time spent feeding (log-transformed to improve model fit) were the dependent variables; arrival order at feeding sites, sex/reproductive state, and the interaction between them were fixed predictors; out-of-sight time per focal sample was an offset variable (mean  $\pm$  SD = 0.7  $\pm$  2.0 min; range = 0–9 min); and subject identity was a random factor to account for the repeated measurements of the same individuals. We divided the ordinal position of focal individuals at arrival to a feeding site by the total number of adults in their groups to account for variation in group size. The feeding behavior of mantled howler monkeys varies as a function of the food item that is consumed (Reynoso-Cruz et al., 2016). Thus, we included the type of consumed food item (i.e., ripe and unripe fruits, mature and young leaves, and flowers) as a control variable. As focal subjects only consumed flowers in two samples we excluded this item from further analysis, resulting in a total of 215 analyzed feeding episodes.

We visually inspected the residual distribution of all models via Q–Q plots which revealed no deviations from linearity; and analyzed residual normality with Shapiro–Wilks tests, which indicated no significant differences from an expected normal distribution (i.e.,  $p > 0.05$  for all tests). Generalized variance inflation factors were low ( $< 3$ ) in all models, indicating no significant collinearity between fixed predictors. We also assessed the relative contribution of fixed predictors relatively to the control and random factors with likelihood ratio tests which in all cases indicated that complete models explained a significantly higher proportion of the variance in the response variables than control and random variables alone (i.e.,  $p < 0.001$  in all tests). We calculated pseudo coefficients of determination of feeding behavior models as an effect size measure. When categorical predictors had a significant effect on feeding measures, we ran post hoc pairwise comparisons with a Tukey

adjustment. All analyses were performed in R 4.2.3 (R Core Team, 2023).

## 3 | RESULTS

### 3.1 | Leadership and arrival at feeding sites

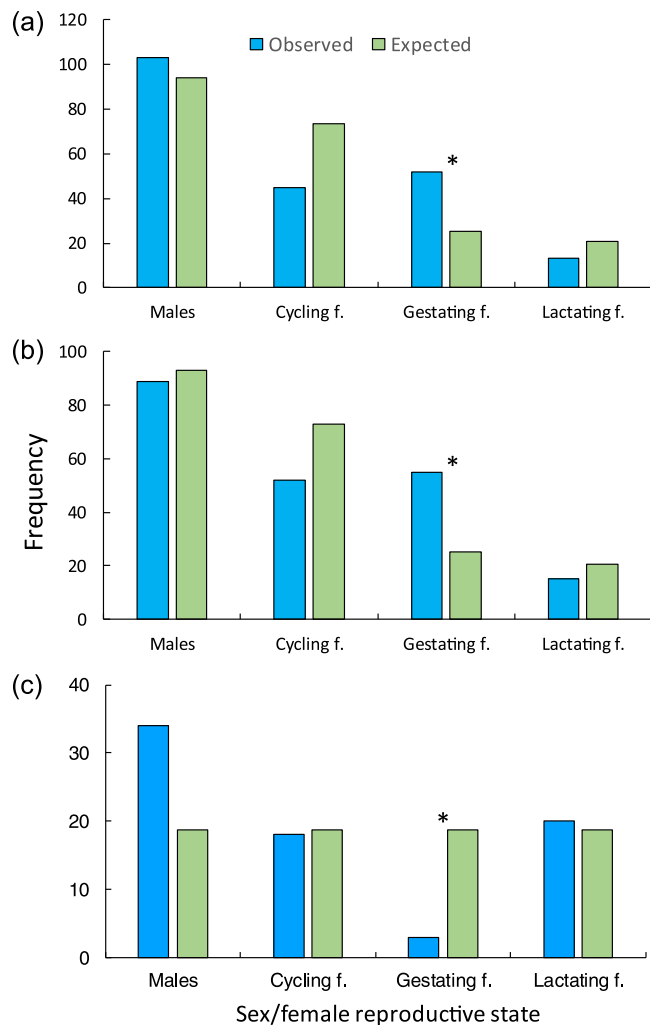
Gestating females led group movements and found (i.e., were the first to arrive at) feeding sites more frequently than expected (Figure 1; Supporting Information S1: Tables 3 & 4). They were, however, also more likely to be replaced by other group members as leaders, usually males (Supporting Information S1: Table 4).

### 3.2 | Arrival order at feeding sites and feeding behavior

Following their arrival at feeding sites, mantled howler monkeys ingested a mean ( $\pm$ SD) of 15.4  $\pm$  39.6 g (range = 0.01–445 g) of food, had a mean bite rate of 2.6  $\pm$  1.8 bites/min (range = 0.08–22.2), and fed for a mean of 18.6  $\pm$  14.5 min (range = 1–87). The mean ( $\pm$ SD) order of arrival at feeding sites showed low variation among sexes/reproductive states ( $\chi^2_{3,211} = 3.7$ ,  $p = 0.293$ ), being the lowest in lactating females (0.34  $\pm$  0.15), followed cycling females (0.39  $\pm$  0.23), gestating females (0.41  $\pm$  0.26), and males (0.44  $\pm$  0.22). The feeding behavior of mantled howler monkeys was not affected by the order of arrival at feeding sites per se (Table 1). However, sex/reproductive state and its interaction with order of arrival influenced feeding behavior measures. First, gestating females had lower food intake rate than cycling females (Figure 2a); lower bite rate than cycling females and males (Figure 2b); and lower feeding time than cycling females (Figure 2c;  $p < 0.05$  for all mentioned pairwise comparisons). Second, gestating females had a pronounced decrease in food intake rate, bite rate, and feeding time as they (progressively) arrived later at feeding sites. These changes were significantly different from those observed for food intake rate in cycling females and males (Figure 2d) and both bite rate and feeding time of males (Figure 2e,f;  $p < 0.05$  for all mentioned pairwise comparisons).

## 4 | DISCUSSION

Our aim was to examine if leadership toward feeding sites varies according to the sex and reproductive state in mantled howler monkeys. Additionally, we investigated variation in feeding behavior depending on the order of arrival at feeding sites and the sex/reproductive state of individuals. Gestating females were more likely than expected to lead group movements toward feeding sites and find feeding sites than females in other reproductive states and males. Yet, they were also more likely to be replaced as leaders. Contrary to our prediction, feeding behavior did not vary as a function of order of arrival per se, but gestating females had the



**FIGURE 1** Observed (blue) and expected (green) frequencies of leadership during a movement toward a feeding site (a), finding a feeding site (b), and being replaced in the leading position during a movement toward a feeding site (c) according to sex/female reproductive state in mantled howler monkeys studied at La Flor de Catemaco. Asterisks indicate category contributing largest proportion of nonrandomness.

lowest food intake rate, bite rate, and feeding time. Additionally, gestating females increased food intake rate, bite rate, and feeding time as they arrived earlier at feeding sites, especially when compared with cycling females and males. We therefore argue that gestating females use leadership and the finder's advantage to enhance their foraging success.

In a previous study we proposed that, while gestating and lactating, females should act as leaders during group movements directed at feeding sites more often than other individuals because these are the most energetically demanding reproductive states; by arriving first, they could enhance foraging success (Ceccarelli et al., 2020). In that study gestating females were in fact the most frequent leaders, which we interpreted as a result of higher nutritional/energetic needs compared with cycling females and males, and of greater mobility compared with lactating females

carrying dependent offspring. Here, we replicated that result, but, contrary to our prediction, we also found that gestating females were more likely to be replaced in the front position during group movements, which questions its interpretation. Our data does not allow assessing the causes underlying the replacement of gestating females as leaders, but the influence of reduced mobility compared to cycling females and males on leadership replacement could be explored in future studies. For instance, it is possible that gap crossing and traveling through sharp slopes is a greater challenge for gestating females than to other individuals due to increased body weight during pregnancy (Garber & Rehg, 1999; Gregory et al., 2014). It is important to note, however, that leadership was mostly stable (i.e., no replacement occurred in 65% of movements), suggesting that there was shared consensus among group members in terms of when and where to travel (Conradt & Roper, 2003; Pyritz et al., 2011).

Regarding lactating females, the question of why they are not leaders or finders more frequently remains unsolved (Ceccarelli et al., 2020), although the small sample size for this reproductive state limits the explanatory power of our analysis. It is possible that, compared to females in other reproductive states, lactating females dedicate more time to rest and vigilance than to locomotion and feeding (Barrett et al., 2006; Dias et al., 2011; Lappan, 2009). Additionally, although individuals at the forefront of the group movement have a higher probability of being the first to arrive at feeding sites and initiate resource exploitation (Boinski, 1991; Erhart & Overdorff, 1999; Fischhoff et al., 2007), they are also more likely to face risks, such as predators or extragroup conspecifics. This may lead lactating females with vulnerable offspring to avoid that position. Similar trends have been observed in female Central American squirrel monkeys (*Saimiri oerstedii*), who are usually highly active in leading group movements at the forefront, but after giving birth, assume more central positions (Boinski, 2000).

Resource finders start food consumption earlier and monopolize a fraction of the items before followers, which should yield benefits in terms of energy/nutrient acquisition (Rita et al., 1997). Our results suggest that the finder's advantage in this species is linked to sex and reproductive state rather than to order of arrival per se, as variation in feeding behavior was related to the sex and reproductive state of individuals and its interaction with order of arrival. Specifically, when arriving first at feeding sites, females had higher food intake rate, bite rate, and feeding time than males, and feeding behavior was similar among females in different reproductive states. This result converges with evidence that it is common for individuals with higher energy requirements, which are typically reproductive or post-reproductive females (Conradt et al., 2009; Fischhoff et al., 2007; King et al., 2008; Rands et al., 2008; Smith et al., 2015, 2020; Sueur et al., 2010), to initiate and lead group movements toward feeding sites (Sueur et al., 2010, 2013).

In our study, it is unlikely that variation between sexes in leadership and finding of feeding sites is linked to differences in knowledge about resource location and availability (Viljoen, 1990), as subjects of both sexes were either translocated to La Flor de Catemaco as adults about twenty years ago or were adult individuals

**TABLE 1** Mixed model results of the influence of arrival order to feeding sites and sex/reproductive state on the feeding behavior of mantled howler monkeys studied at La Flor de Catemaco ( $n = 215$  feeding episodes).

Variable/predictor	Term	$\chi^2$	$p$	95% CI	
				Lower	Upper
<b>Food intake rate (0.23/0.23)<sup>a</sup></b>					
Arrival order		1.1	0.286	-2.75	4.91
Sex/reproductive state <sup>b</sup>		24.3	<0.001		
	Gestating			-2.58	2.71
	Lactating			-3.99	4.71
	Male			-3.91	1.02
Arrival order $\times$ sex/reproductive state <sup>b</sup>		12.8	0.005		
	Gestating			-14.47	-3.16
	Lactating			-14.54	8.34
	Male			-4.67	5.82
Food item <sup>c</sup>		29.6	<0.001		
	Ripe fruit			2.43	6.53
	Unripe fruit			-1.29	3.44
	Young leaves			1.36	5.54
<b>Bite rate (0.18/0.18)</b>					
Arrival order		1.5	0.209	-3.99	3.56
Sex/reproductive state		16.3	<0.001		
	Gestating			-2.32	2.89
	Lactating			-3.86	4.71
	Male			-4.20	0.67
Arrival order $\times$ sex/reproductive state		12.7	0.005		
	Gestating			-12.99	-1.86
	Lactating			-13.01	9.52
	Male			-2.80	7.54
Food item		20.1	<0.001		
	Ripe fruit			1.84	5.88
	Unripe fruit			-1.01	3.65
	Young leaves			1.12	5.23
<b>Feeding time (0.20/0.20)</b>					
Arrival order		1.3	0.253	-3.92	3.59
Sex/reproductive state		18.9	<0.001		
	Gestating			-2.49	2.70
	Lactating			-3.83	4.70
	Male			-4.63	0.21
Arrival order $\times$ sex/reproductive state		14.2	0.003		
	Gestating			-13.13	-2.04
	Lactating			-13.43	9.01
	Male			-2.40	7.90



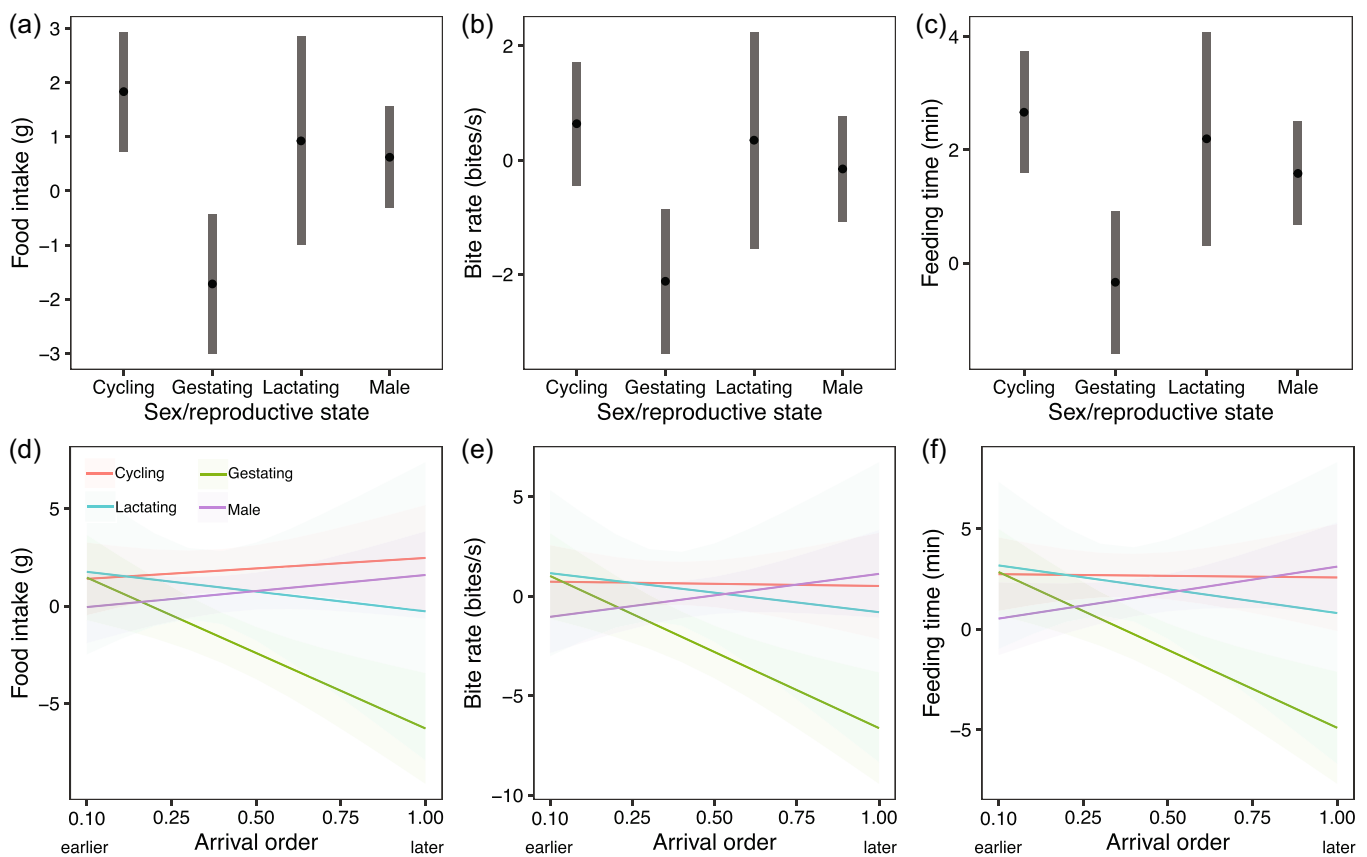
TABLE 1 (Continued)

Variable/predictor	Term	$\chi^2$	<i>p</i>	95% CI	
				Lower	Upper
Food item		22.4	<0.001		
	Ripe fruit			1.46	5.49
	Unripe fruit			-1.99	2.64
	Young leaves			0.48	4.57

<sup>a</sup>Numbers in parenthesis represent pseudo coefficients of determination of models. The first value is the marginal coefficient of determination (i.e., deviance explained by the fixed predictors), and the second value is the conditional coefficient of determination (i.e., deviance explained by fixed and random predictors combined).

<sup>b</sup>Comparisons against the cycling female category.

<sup>c</sup>Comparisons against the mature leaf category.



**FIGURE 2** The influence of sex/reproductive state (a–c) and of the interaction between sex/reproductive state and arrival order at feeding sites (d–f) on the feeding behavior of mantled howler monkeys studied at La Flor de Catemaco: food intake rate (a and d); bite rate (b and e); and feeding time (c and f). In (a–c), black dots are the predicted estimates and gray rectangles are their 95% confidence intervals. In (d–f), solid lines are the predicted estimates and shaded areas are their 95% confidence intervals. In (d–f), arrival order (x-axis) was normalized between 0.1 (being the finder of a feeding site) and 1 (being the last group member to arrive at the site).

born at the site (Dias et al., 2023). Additionally, individual identity had a limited influence on feeding behavior, suggesting that, besides experience, variation in other intrinsic attributes such as age, dominance rank, or social relationships (Fichtel et al., 2011; King et al., 2009) does not explain our results. Additional proximate influences affecting the feeding behavior of mantled howler

monkeys, which were not addressed in our study, warrant further investigation. For example, factors like satiation (Bell, 1991) could play a significant role. If gestating females consistently lead early morning group movements toward feeding sites where they can satiate, they might have decreased motivation to initiate group movements later in the day. Furthermore, the dynamics of leadership

and feeding behavior may be intertwined with variables such as food availability per feeding patch, the type of food consumed, and the time elapsed between successive feeding bouts (Plante et al., 2014; Righini et al., 2020; Snaith & Chapman, 2005).

Gestating females had increasing food intake rate, bite rate, and feeding time as they arrived earlier at feeding sites. If these trends were associated with higher energy/nutrient intake, frequent leadership of group movements toward feeding sites may enhance their foraging success. The fact that in this species C-peptide concentrations peak during gestation, indicating high energy balance (Rangel Negrín et al., 2022), supports the argument that females use leadership and the finder's advantage to boost foraging success, as reported for other primates (e.g., Boinski, 1991, 1993; Erhart & Overdorff, 1999; Overdorff et al., 2005; Trillmich et al., 2004). Given that food preferences and digestive physiology may vary through the reproductive cycle (e.g., Emery Thompson, 2013; Mallott et al., 2020), future assessments of the nutritional and secondary metabolite composition of foods consumed by females in relation to their reproductive state and order of arrival at feeding sites may provide further insight into leadership and the finder's advantage dynamics in this species.

#### AUTHOR CONTRIBUTIONS

**Aylén D. Giannetti-Domínguez:** Conceptualization (equal); data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); validation (equal); visualization (equal); writing—original draft (equal). **Ariadna Rangel-Negrín:** Conceptualization (equal); funding acquisition (equal); project administration (equal); resources (equal); supervision (equal); validation (equal); writing—review and editing (equal). **Alejandro Coyohua-Fuentes:** Data curation (equal); investigation (equal); writing—review and editing (equal). **Pedro A. D. Dias:** Conceptualization (equal); formal analysis (equal); funding acquisition (equal); methodology (equal); project administration (equal); resources (equal); supervision (equal); visualization (equal); writing—original draft (equal); writing—review and editing (equal).

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#### CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

#### DATA AVAILABILITY STATEMENT

Data that support this study is available in the article and accompanying online supplementary material.

#### ETHICS STATEMENT

This study was noninvasive, adhered to the ASP Code of Best Practices in Field Primatology, and to the ASP Principles for the Ethical Treatment of Nonhuman Primates. The research was approved by permits SGPA/DGVS/13528/19 and SGPA/DGVS/04015/21 from Secretaría de Medio Ambiente y Recursos Naturales (México).

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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