

RESEARCH ARTICLE

Sex differences in leadership during group movement in mantled howler monkeys (*Alouatta palliata*)

Enrico Ceccarelli | Ariadna Rangel Negrín | Alejandro Coyohua-Fuentes | Domingo Canales-Espinosa | Pedro Américo D. Dias 

Primate Behavioral Ecology Lab, Instituto de Neuroetología, Universidad Veracruzana, Xalapa, México

Correspondence

Pedro Américo D. Dias, Primate Behavioral Ecology Lab, Instituto de Neuroetología, Universidad Veracruzana, Xalapa, CP 91190, México.
Email: pdias@uv.mx

Funding information

Universidad Veracruzana, Grant/Award Number: Apoyo de la DGDAIE a CA-UV-25; Consejo Nacional de Ciencia y Tecnología, Grant/Award Numbers: 254217, 592163

Abstract

Benefits of group life depend in large part on whether animals remain cohesive, which often requires collective decisions about where and when to move. During a group movement, the leader may be considered as the individual occupying the vanguard position of the group progression, when its movement evokes following by other group members. In nondespotic societies, individuals with greater incentives to move frequently are leaders. During 15 months of observations (1,712 contact hours), we investigated two mantled howler monkey (*Alouatta palliata*) groups at La Flor de Catemaco (Los Tuxtlas, Mexico) to examine whether sex and female reproductive state influenced leadership likelihood in two contexts: movements toward feeding trees; movements associated with loud calls, a group-defense behavior used by males of this genus. Females led and occupied forward positions during group movements toward feeding trees more often than adult males. Adult females led these movements more frequently when they were gestating than when they were lactating or cycling. There were no differences between sexes in the leadership of group movements associated with loud calls. Leadership by gestating females is perhaps the result of their higher nutritional/energetic needs when compared with cycling females, and of their greater mobility when compared with lactating females carrying dependent offspring. Female leadership during movements toward feeding trees may be a mechanism to optimize access to food resources in mantled howler monkeys.

KEYWORDS

collective behavior, group defense, leadership, movement, progression order

1 | INTRODUCTION

Collective movements play an important role in determining the structure and dynamics of populations and ecosystems, as well as in the evolution and diversity of organisms (Aves, Insecta, and Mammalia: Bullock, Kenward, & Hails, 2002; Clobert, Danchin, Dhondt, & Nichols, 2001; Dingle, 1996; Swingland & Greenwood, 1983). In heterogeneous groups of individuals, members often differ in their physiological needs and abilities (Primates: McCabe &

Fedigan, 2007; Equidae: National Research Council, 1989; Bovidae: Prins, 1996; Ursidae: Robbins et al., 2007), and to maintain group cohesion during movements, they must make decisions despite all possible interindividual conflicts of interest (Conradt & Roper, 2003, 2005).

In group movements, the leader may be defined as the subject influencing and coordinating movement by other group members (Pyritz, King, Sœur, & Fichtel, 2011a). Although spatial position during group movement is not necessarily explicative to the role of

leader (Kummer, 1968; Pyritz, Fichtel, & Kappeler, 2010), individuals occupying the first position of the group progression eliciting following behavior by other group members may be considered leaders (Pyritz et al., 2011a; Rhine & Westlund, 1981; Watts, 1994). Individuals that occupy the front positions of group progressions can benefit from having greater control over time, distance, and direction of movement. They can also have priority of access to food resources and thus optimize energy and nutrient intake, improving their physical condition and, potentially, their long-term reproductive success (Barelli, Boesch, Heistermann, & Reichard, 2008; Beauchamp, 2000; Boinski, 1991; Erhart & Overdorff, 1999). Under distributed leadership (i.e., different group members act as leaders), individual attributes such as age, sex, and reproductive state may influence the likelihood of leading group movements (Fichtel, Pyritz, & Kappeler, 2011; Fischhoff et al., 2007; King, Johnson, & van Vugt, 2009; Leca, Gunst, Thierry, & Petit, 2003; Stueckle & Zinner, 2008).

Female mammals face higher metabolic demands during gestation and lactation than at other times (Gittleman & Thompson, 1988; Speakman, 2008). In primates, daily energy requirements may increase by 25% for gestating females and by 50–100% for lactating females (Key & Ross, 1999; Portman, 1970). These requirements are subsidized by changes in energy and nutrient acquisition (Kunz & Orrell, 2004), either through the metabolization of fat reserves or increases in food intake (Dufour & Sauter, 2002; Emery Thompson, 2013). The latter could explain why in several primate species females lead group movements more often than males (e.g., *Eulemur rufifrons*: Pyritz, Kappeler, & Fichtel, 2011; *Hylobates lar*: Barelli et al., 2008; *Propithecus diadema edwardsi* and *Eulemur fulvus rufus*: Erhart & Overdorff, 1999; *Propithecus verreauxi*: Trillmich, Fichtel, & Kappeler, 2004) and gestating and lactating females lead more often than other group members (*Eulemur flavifrons*: Volampeno, Masters, & Downs, 2011). In this context, as leaders may decide which food sources are searched for and exploited (i.e., “finder’s advantage”: Giraldeau & Caraco, 2000), female leadership could be a mechanism to increase access to food resources that allow coping with high nutrient/energy requirements.

Male leadership during group movements may be interpreted as a reproductive strategy. Mountain gorilla silverback males (*Gorilla gorilla beringei*), for instance, lead group movements to avoid lone males (Watts, 1994), and spider monkey males (*Ateles geoffroyi*) frequently lead all-male subgroups toward home range limits (Chapman, 1990), where raids against neighboring communities may increase reproductive opportunities (e.g., finding sexually receptive females: Aureli, Schaffner, Verpooten, Slater, & Ramos-Fernández, 2006). Conversely, male positioning during movement has been associated with group defense in risk situations (Petit & Bon, 2010), such as encounters with extra group individuals (Rhine & Tilson, 1987; Rhine & Westlund, 1981). Given that males from several species use long-range vocalizations (henceforth loud calls) to signal their location and competitive potential (e.g., *Cebus apella*: Robinson, 1982; *Cercocebus albigena*, *Cercopithecus mitis*, *C. ascanius*, *C. mona*: Waser & Waser, 1977; *Colobus guereza*: Harris, 2006; *Hylobates agilis*, *H. concolor*, *H. booblock*, *H. klossii*, *H. lar*: Cowlshaw,

1996; *Leontopithecus rosalia*: Halloy & Kleiman, 1994; *Nomascus concolor*: Peng-Fei, Wen, Sheng, & Xue-Long, 2009; *Presbytis thomasi*: Steenbeek, Assink, & Wich, 1999), it could be expected that movements associated with loud calls are more likely led by males than females.

In this study, we examine leadership behavior during group movements in mantled howler monkeys (*Alouatta palliata*). Mantled howler monkeys live in multimale–multifemale groups that are usually spatiotemporally stable (Di Fiore & Campbell, 2007). As in other howler monkey species (*A. caraya*: Fernández, Kowalewski, & Zunino, 2013), adult group members have been observed to lead group movements more often than immature individuals (Costello, 1991), probably because the latter have limited knowledge of their home ranges and of resources therein (Janson & van Schaik, 1993). Mantled howler monkeys are classified as nonseasonal breeders (Di Bitetti & Janson, 2000) and births may occur in any month of the year (Estrada, 1982; Jones, 1980). Their diet varies from frugivorous to folivorous depending on seasonality in food item availability (Dias & Rangel-Negrín, 2015). During gestation and lactation mantled howler monkey females increase the consumption of fats, proteins, and energy (Serio-Silva, Hernández-Salazar, & Rico-Gray, 1999), and have higher glucocorticoid hormone concentrations (independently of psychosocial activation of the stress axis: Dias, Coyohua-Fuentes, Canales-Espinosa, Chavira-Ramírez, & Rangel-Negrín, 2017) than cycling females. Female energetic condition (assessed via urinary C-peptide concentrations) does not vary significantly among reproductive stages, although gestating females tend to have higher physical condition than other females (Cano-Huertes et al., 2017). This evidence suggests that female mantled howler monkeys meet the increased metabolic demands of gestation and lactation through diet adjustments and metabolization of energy reserves.

Adult howler monkey males produce loud calls periodically during the day (Baldwin & Baldwin, 1976). The loud calls of howler monkeys seem to be multifunctional, as they have been associated with mutual avoidance among neighboring groups (Whitehead, 1987), advertising of territory occupation (da Cunha & Byrne, 2006), advertising of competitive ability (Kitchen, 2004, 2006; Sekulic, 1982), and border defense (da Cunha & Jalles-Filho, 2007). Simulated home range invasion elicits vocal responses and group movements led by males (da Cunha & Byrne, 2006; Whitehead, 1987), and males have been observed leading groups during intergroup encounters (Fernández et al., 2013), suggesting that leadership by male howler monkeys could be part of a group-defense strategy.

Our aim was to determine variation between sexes in leadership likelihood during group movements in mantled howler monkeys. We hypothesized that leadership is a behavioral strategy that adult males and females exhibit differently depending on the context. We made three predictions of this hypothesis. First, to have greater control over the type and quality of food sought and consumed, females should lead group movements toward feeding trees more often than males. Second, as reproductive females face higher nutrient and energy demands than nonreproductive females, gestating and lactating females should lead group movements toward feeding

trees more often than cycling females. Third, because the main mechanism of group defense by males is loud calling, males should lead group movements associated with the occurrence of loud calls more often than females.

2 | METHODS

2.1 | Ethical note

Our study was noninvasive and adhered to the ASP Code of Best Practices in Field Primatology and to the ASP Principles for the Ethical Treatment of Nonhuman Primates. Research protocols were approved by the Secretaria de Medio Ambiente y Recursos Naturales (permits SGPA/DGVS/10637/11 and SGPA/DGVS/04999/14) and complied to the legal requirements of Mexican law (NOM-059-SEMARNAT-2010).

2.2 | Study site and subjects

We conducted our study at La Flor de Catemaco (18°26'43" N, 95°02'49" W) located within the Los Tuxtlas region in Veracruz (Mexico). This site is a 250-ha ranch that mainly produces ornamental palms in the shade of a 100-ha lowland tropical high evergreen rain forest. The forest floor and understory are disturbed by the palm plantations, but the canopy and emergent strata correspond to mature forest, both in terms of tree structure and composition (Bongers, Popma, Meave, & Carabias, 1988). Arboreal fauna at La Flor de Catemaco is diverse, including, in addition to mantled howler monkeys, other mammals (e.g., coatis: *Nasua narica*; Mexican hairy dwarf porcupines: *Coendou mexicanus*; tamanduas: *Tamandua mexicana*), birds (e.g., keel-billed toucans: *Ramphastos sulfuratus*; ornate hawk-eagles: *Spizaetus ornatus*; scarlet macaws: *Ara macao*), reptiles (e.g., Mexican parrot snakes: *Leptophis mexicanus*), and insects (e.g., leaf-cutter ants: *Atta mexicana*). The climate is tropical, with mean annual rainfall of 2,600 mm and a mean ambient temperature of 26°C.

The mantled howler monkey population of La Flor de Catemaco was established in 2004 through the translocation of two groups into the area (Aguilar-Cucurachi et al., 2010; Shedden-González & Rodríguez-Luna, 2010). The population has been monitored since, and by March 2017 (when this study was finished), 20 mantled howler monkeys lived in three groups and four individuals lived solitarily. We studied the two mantled howler monkey groups that have been observed since translocation: G1, with three adult males, three adult females, and one infant; G2, comprising three adult males, four adult females, and three infants. Our study concentrated on the 13 adult subjects, which were fully habituated to the presence of researchers and were easily recognized through anatomical and physiognomic characteristics.

We classified adult females as cycling, gestating, or lactating. We based this classification on the observation of births and infants ages

6 months before, during, and 6 months after the study. In this species, 6 months is the mean duration of gestation (Glander, 1980) and of the period during which milk is the only source of nutrition for infants (Balcells & Veà, 2009). Thus, for each study month females were classified as (a) gestating, during the 6 months before the birth of their infants; (b) lactating, during the first 6 months postpartum; (c) cycling, when they were neither gestating nor lactating. During the 15-month data collection period, we recorded 54 cycling female/months, 19 gestation female/months, and 24 lactation female/months (Table S1).

2.3 | Behavioral data collection

From January 2016 to March 2017, we observed each study group 4 days per week, from 6:00 to 18:00 hr. Using all-occurrences sampling (Altmann, 1974), we (three observers) recorded all instances of group movement, for a total of 1,712 hr. We defined group movement as every time >50% of the adult group members moved to a different tree and engaged in a different activity from that in the starting tree. We considered a movement to end when $\geq 75\%$ of the adults stayed in the same tree for at least 15 min. For this study, we focused on two types of group movements: (a) movements toward feeding trees, which ended in a feeding tree where $\geq 75\%$ of adult individuals fed within 15 min after the end of the movement ($N = 286$ events); (b) movements associated with vocalizations, in which at least one group male loud-called during or up to 15 min after the end of a movement ($N = 275$ events), and the movement did not finish in a feeding tree.

2.4 | Leadership measures

We defined two leadership measures. The first measure was being at the front of the group during group movements. For each group movement, we recorded the identity of the leader, defined as the first group member to move from the tree at movement onset. We also recorded the identity and order of followers and any occasion in which a new individual occupied the leading position. In the analysis, we only used movements without leader replacement (movements toward feeding trees = 244; movements associated with loud calls = 242).

The second measure was the position of followers (i.e., individuals that occupied nonleading positions) during group movements, calculated as a progression order index (Barelli et al., 2008). For each group movement, we standardized the position of each subject in the sequence of followers by dividing its position (minus one) by the number of subjects in the sequence (minus one). We averaged progression order indexes per individual per month, excluding movements in which it had the leading position. To assess whether individuals most frequently assumed front or back positions during group movements, subjects with monthly indexes < 0.5 were categorized as usually occupying front positions, whereas those with average monthly indexes > 0.5 were categorized as usually occupying back positions.

2.5 | Data analysis

To test our predictions, we used generalized linear mixed models (GLMM) with binomial error distributions. To test the first prediction, we ran two models. In the first, the number of times each individual moved toward a feeding tree as a leader and as a follower per month was added as a two-vector response variable (using function “cbind” in R: R Core Team, 2019) and the fixed predictor was sex. In the second model, the mean individual monthly progression order index during movements toward feeding trees categorized as “front” or “back” was the dependent variable and sex was the fixed predictor. We used two models to test the second prediction: in the first, the number of times each individual moved toward feeding trees as leader and as follower per month was added as a two-vector response variable and the fixed predictor was female reproductive state; in the second, mean individual monthly progression order index during movements toward feeding trees categorized as “front” or “back” was the dependent variable and female reproductive state was the fixed predictor. Finally, we ran two models for the third prediction: first, the number of times each individual moved in association with the occurrence of loud calls as leader and as follower per month was added as a two-vector response variable, and sex as the fixed predictor; second, mean individual monthly progression order index during movements associated with the occurrence of loud calls, categorized as “front” or “back”, was the dependent variable and sex was the fixed predictor. In all models, subject identity was included as a random factor to account for the repeated sampling of individuals through time.

During the study, there was an uneven number of subjects of each sex and of females in each reproductive state category. To determine if results were biased in favor of categories with more data points in the analysis, we calculated a control variable as the relative contribution of each category to the data set by dividing the number of individuals in each particular category (i.e., male/female in tests of the first and third predictions and cycling/gestating/lactating females in tests of the second prediction) per month by the number of individuals in the category with the most individuals in that month. We prepared two sets of models, one with the models described in the previous paragraph, and another one in which the control variable was added as a fixed factor. We compared models for each prediction with and without the control variable with a likelihood ratio test and in all cases, the comparisons were nonsignificant ($p > .05$). Thus, as variation in the number of subjects contributing data to each category in each month did not affect results, for simplicity we present model results without the control variable.

To determine whether the random factor (i.e., identity) had a stronger impact on dependent variables than fixed factors (Pinheiro & Bates, 2000), we compared all complete models (i.e., with fixed and random factors) with a null model including only the response and the random variables with a likelihood ratio test. In all cases, complete and null models were significantly different ($p < .001$), indicating that the random factor had a lower influence on variation in dependent variables than fixed factors. When the reproductive

state had a significant effect in response variables, we ran post hoc Tukey pairwise comparisons. All analyses were performed with R 3.6.0 (R Core Team, 2019) using packages “car” 3.0-3 (Fox, Weisberg, & Price, 2019), “lme4” 1.1-21 (Bates, Maechler, Bolker, & Walker, 2019), and “multcomp” 1.4-10 (Hothorn, Bretz, & Westfall, 2019).

3 | RESULTS

3.1 | Movements toward feeding trees

Females were more likely than males to lead group movements toward feeding trees (GLMM: $\beta = -1.22$, 95% C.I. = -1.73 – (-0.71) , $Z = 5.11$, $p < .001$; Figure 1a). Gestating females led group movements more often than females in other reproductive states (Figure 1b and Table 1). Concerning the position of non-leaders during group movements toward feeding trees, regardless of reproductive state, females occupied front positions more frequently than males (GLMM: $\beta = 2.40$, 95% C.I. = 1.28 – 3.74 , $Z = 4.20$, $p < .001$; Figure 2). The reproductive state was not associated with significant variation in the likelihood of females occupying front or back positions during group movements toward feeding trees (Table 1).

3.2 | Movements associated with loud calls

There were no significant differences between sexes in the likelihood of leading (GLMM: $\beta = .17$, 95% C.I. = -0.34 – 0.67 , $Z = 0.72$, $p = .470$) or occupying front/back positions (GLMM: $\beta = -.09$, 95% C.I. = -1.55 – 1.29 , $Z = -0.14$, $p = .887$) in group movements associated with loud calls.

4 | DISCUSSION

In this study, we observed that all adult mantled howler monkeys belonging to two groups successfully (i.e., were followed by other group members) led group movements toward feeding trees and movements associated with loud calls. Adult females led their groups and occupied front positions during movements toward feeding trees more frequently than adult males. Additionally, females were more likely to lead groups to feeding trees when gestating than when cycling or lactating. There were no differences between sexes in the likelihood of leading groups during movements associated with loud calls.

In several primate species, differences in feeding patterns between sexes have been documented, with females spending more time feeding, having higher feeding rates, and consuming more food than males (e.g., *Pongo pygmaeus*: Rodman, 1977; *C. albigena*: Waser, 1977; *Aotus trivirgatus* and *Callicebus moloch*: Wright, 1984; *Saimiri oerstedii*: Boinski, 1987; *Cebus capucinus*: Rose, 1994; *C. olivaceus*: Fragaszy & Boinski, 1995). One possible mechanism underlying such differences could be female leadership of group movements toward feeding trees, which may yield greater control over the type and quality of food sought and consumed (Barelli et al., 2008; Boinski, 2000; Fischhoff et al., 2007; Overdorff, Erhart, &

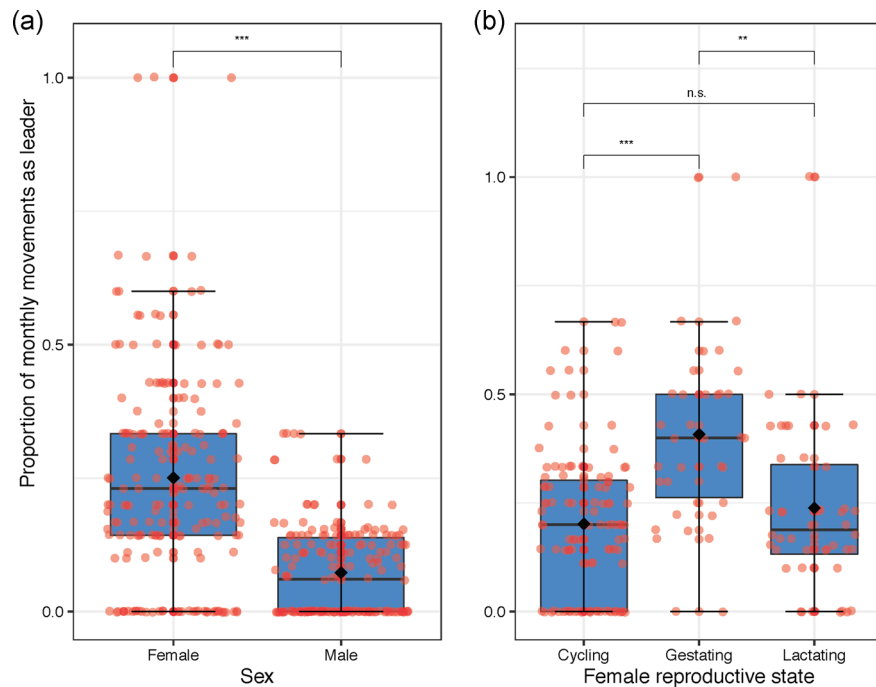


FIGURE 1 Differences between sexes (a) and among females in different reproductive states (b) in leadership during group movements toward feeding trees in two groups of mantled howler monkeys studied at La Flor de Catemaco (Mexico), between January 2016 and March 2017. For illustrating purposes, leadership is represented as the proportion of monthly movements led by each individual. Thick lines inside the boxes are the medians; black diamonds are the means; box limits are the 25th and 75th percentiles; whiskers indicate 1.5*interquartile ranges. Data points are plotted as red circles. n.s. = nonsignificant, ** $p < .01$, *** $p < .001$. In B, pairwise comparisons calculated with Tukey tests. In A, $N = 180$ movements from 13 subjects; in B, $N = 94$ movements from seven subjects

TABLE 1 GLMM results of variation in the likelihood of leading (A) and occupying front/back positions (B) during group movements toward feeding trees according to female reproductive state in two groups of mantled howler monkeys studied at La Flor de Catemaco (Mexico), between January 2016 and March 2017 ($N = 94$ group movements)

| Model/term | β | SE | 95% C.I. | Z | p |
|---------------------------------|---------|------|----------------|-------|-------|
| A) Leading position | | | | | |
| Intercept | -1.44 | 0.20 | -1.92 to -1.06 | -7.13 | <.001 |
| Reproductive state ^a | | | | | |
| Gestating | 0.81 | 0.24 | 0.33 to 1.29 | 3.31 | <.001 |
| Lactating | 0.29 | 0.26 | -0.21 to 0.80 | 1.10 | .270 |
| B) Follower position | | | | | |
| Intercept | -1.12 | 0.45 | -2.16 to -0.22 | -2.52 | .012 |
| Reproductive state ^a | | | | | |
| Gestating | -1.57 | 1.10 | -4.55 to 0.31 | -1.42 | .156 |
| Lactating | -.05 | 0.61 | -1.33 to 1.60 | -0.09 | .932 |

Abbreviation: GLMM, generalized linear mixed models.

^aComparisons against the cycling female category.

Mutschler, 2005). Future research on this putative mechanism, as applied to mantled howler monkeys, could examine interindividual variation in access to food, in the intake of different types of foods, and on the nutritional contents of the ingested foods.

Adult females led group movements toward feeding trees more frequently when they were gestating than when they were lactating or cycling, although reproductive state did not affect the likelihood of

occupying front or back positions when females were followers. Both theoretical models and empirical studies have emphasized the importance of energy requirements in the probability of individuals acting as leaders (King & Sueur, 2011a, 2011b). In cohesive social units, variation in energy reserves results in divergent behavioral roles: individuals with lower energy reserves act as “pace-makers” of movement, and may eventually emerge as leaders (Rands, Cowlshaw, Pettifor, Rowcliffe, & Johnstone, 2003). The energetics of female reproduction seem to be an important factor in determining female leadership in group movements (Conradt, Krause, Couzin, & Roper, 2009; Sueur, Deneubourg, Petit, & Couzin, 2010), and may result from the relatively high motivation of reproductive females to find food resources, as they normally require more energy than males for reproduction (Emery Thompson, 2013; Erhart & Overdorff, 1999; Richard, Dewar, Schwartz, & Ratsirarson, 2000), a pattern also observed in non-primate species (e.g., *Equus burchelli*: Fischhoff et al., 2007, *Mungos mungo*: Furrer, Kunc, & Manser, 2012; *Suricata suricatta*: Turbé, 2006). Higher motivation to reach food resources could explain why gestating and lactating females of this species tend to have higher physical condition than cycling females (Cano-Huertes et al., 2017; Dias et al., 2017).

Lactating females led group movements to feeding trees less frequently than gestating females. This may be associated with the observed trend of lactating primate females to spend, compared to females in other reproductive states, a lower proportion of time moving and feeding but more time resting or in vigilance (*Alouatta*

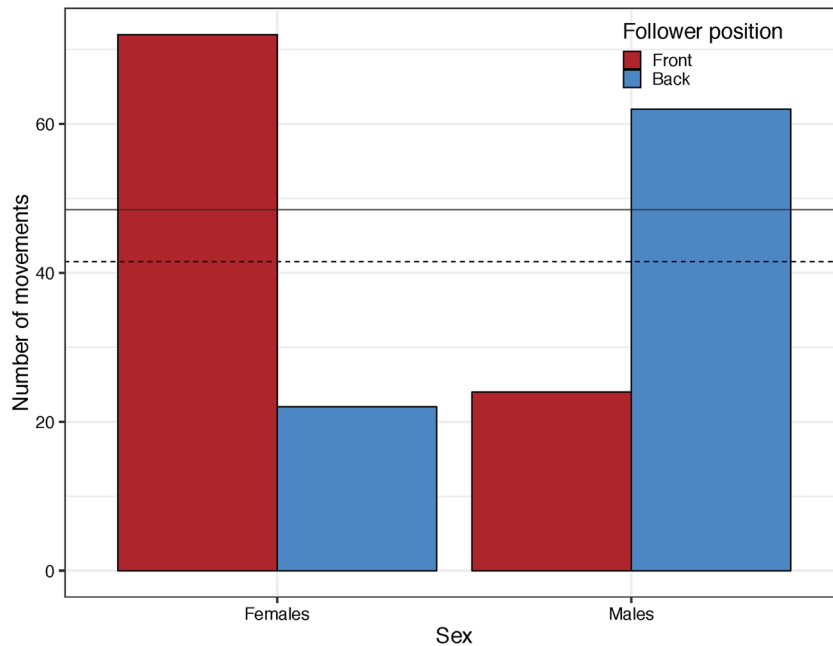


FIGURE 2 Differences between sexes in non-leading positions occupied during group movements toward feeding trees in two groups of mantled howler monkeys studied at La Flor de Catemaco (Mexico), between January 2016 and March 2017. For illustration purposes, the expected number of movements per position per sex under a 50:50% situation is represented as lines (solid = females, dashed = males), corrected by the total number of sampled subjects of each sex (females = 7 subjects, males = 6). $N = 180$ movements

pigra: Dias, Rangel-Negrín & Canales-Espinosa, 2011; *Symphalangus syndactylus*: Lappan, 2009; *Papio hamadryas ursinus*: Barrett, Halliday, & Henzi, 2006). Increased resting time may operate as an efficient strategy to store and save energy (Dasilva, 1992; Dunbar & Sharman, 1984), which is required for milk production and maternal care (Emery Thompson, 2013). Given that in this species maternal behavior varies through lactation (e.g., Dias, Coyohua-Fuentes, Canales-Espinosa, Chavira-Ramírez, & Rangel-Negrín, 2018), it remains to be determined whether leadership patterns in lactating females vary according to infant age through the examination of a larger sample of females.

Our results do not support the prediction that leadership during movements associated with loud calls is part of a group-defense strategy by male howler monkeys. It is possible that, instead of mobilizing their groups to reach specific areas where loud calls are given, males vocalize depending on group location (da Cunha & Byrne, 2006; Fernández et al., 2013; Sekulic, 1982; Whitehead, 1989). For instance, black-and-gold howler monkey (*A. caraya*) males are more likely to lead movements when other groups come into visual contact (Fernández et al., 2013). Thus, although male leadership during movements may be part of a group-defense strategy in howler monkeys (da Cunha & Byrne, 2006; Fernández et al., 2013; Sekulic, 1982; Whitehead, 1989), it is not directly associated with loud calls.

In conclusion, we found evidence of sexual asymmetry in leading during group movement toward feeding trees, which suggests that female mantled howler monkeys use leadership as a mechanism to optimize access to food. Leadership in this context was particularly frequent in gestating females, perhaps as a result of their higher nutritional/energetic needs when compared with cycling females, and of their greater mobility when compared with lactating females carrying dependent offspring. Our results indicate that males do not lead movements associated with the production of loud calls.

ACKNOWLEDGMENTS

The authors thank P. Cruz Miros and several volunteers and students for their invaluable help during fieldwork. La Flor de Catemaco granted permission to work at this site, and Ing. J. L. Ponce Puente facilitated our work in a variety of ways. This study was supported by Universidad Veracruzana and Conacyt (beca doctoral 592163; proyecto ciencia básica 254217). A. Rangel Negrín and P. A. D. Dias were supported by a grant to CA-UV-25 from the Dirección General de Desarrollo Académico e Innovación Educativa, Universidad Veracruzana (México) while preparing this manuscript. A. Rangel-Negrín and P. A. D. Dias thank Mariana and Fernando for constant support and inspiration to study primate behavior. The authors thank Prof. M. A. Norconk and two anonymous reviewers for their constructive and helpful comments that greatly improved this manuscript.

CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

DATA AVAILABILITY STATEMENT

Data that support the findings of this study are available from the corresponding author at a reasonable request.

ORCID

Pedro Américo D. Dias  <http://orcid.org/0000-0002-2919-6479>

REFERENCES

Aguilar-Cucurachi, M. A., Dias, P. A. D., Rangel-Negrin, A., Chavira, R., Boeck, L., & Canales-Espinosa, D. (2010). Preliminary evidence of accumulation

- of stress during translocation in mantled howlers. *American Journal of Primatology*, 72, 805–810. <https://doi.org/10.1002/ajp.20841>
- Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, 49, 227–267. <https://doi.org/10.1163/156853974x00534>
- Aureli, F., Schaffner, C. M., Verpooten, J., Slater, K., & Ramos-Fernández, G. (2006). Raiding parties of male spider monkeys: Insights into human warfare? *American Journal of Physical Anthropology*, 131, 486–497. <https://doi.org/10.1002/ajpa.20451>
- Balcells, C., & Veà, J. J. (2009). Developmental stages in the howler monkey subspecies *Alouatta palliata mexicana*: A new classification using age-sex categories. *Neotropical Primates*, 16, 1–8. <https://doi.org/10.1896/044.016.0101>
- Baldwin, J. D., & Baldwin, J. I. (1976). Vocalizations of howling monkeys (*Alouatta palliata*) in southwestern Panama. *Folia Primatologica*, 26, 81–108. <https://doi.org/10.1159/000155733>
- Barelli, C., Boesch, C., Heistermann, M., & Reichard, U. H. (2008). Female white-handed gibbons (*Hylobates lar*) lead group movements and have priority of access to food resources. *Behaviour*, 145, 965–981. <https://doi.org/10.1163/156853908784089243>
- Barrett, L., Halliday, J., & Henzi, S. P. (2006). The ecology of motherhood: The structuring of lactation costs by chacma baboons. *Journal of Animal Ecology*, 75, 875–886. <https://doi.org/10.1111/j.1365-2656.2006.01105.x>
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2019). Package 'lme4'. Retrieved from <https://cran.r-project.org/web/packages/lme4/lme4.pdf>
- Beauchamp, G. (2000). Individual differences in activity and exploration influence leadership in pairs of foraging zebra finches. *Behaviour*, 137, 301–314. <https://doi.org/10.1163/156853900502097>
- Boinski, S. (1987). Habitat use by squirrel monkeys (*Saimiri oerstedii*) in Costa Rica. *Folia Primatologica*, 49, 151–167. <https://doi.org/10.1159/000156319>
- Boinski, S. (1991). The coordination of spatial position: A field study of the vocal behavior of adult female squirrel monkeys. *Animal Behaviour*, 41, 89–102. [https://doi.org/10.1016/s0003-3472\(05\)80505-6](https://doi.org/10.1016/s0003-3472(05)80505-6)
- Boinski, S. (2000). Social manipulation within and between troops mediates primate group movement. In S. Boinski & P. A. Garber (Eds.), *On the move: How and why animals travel in groups* (pp. 421–469). Chicago, IL: University of Chicago Press.
- Bongers, F., Popma, J., Meave, J., & Carabias, J. (1988). Structure and floristic composition of the lowland rain forest of Los Tuxtlas, Mexico. *Plant Ecology*, 74, 55–80. <https://doi.org/10.1007/BF00045614>
- Bullock, J. M., Kenward, R. E., & Hails, R. (2002). *Dispersal Ecology*. Malden, MA: Blackwell.
- Cano-Huertes, B., Rangel-Negrín, A., Coyohua-Fuentes, A., Chavira-Ramírez, D. R., Canales-Espinosa, D., & Dias, P. A. D. (2017). Reproductive energetics of female mantled howler monkeys (*Alouatta palliata*). *International Journal of Primatology*, 38, 942–961. <https://doi.org/10.1007/s1076>
- Chapman, C. A. (1990). Association patterns of spider monkeys: The influence of ecology and sex on social organization. *Behavioral Ecology and Sociobiology*, 26, 409–414. <https://doi.org/10.1007/bf00170898>
- Clobert, J., Danchin, E., Dhondt, A. A., & Nichols, J. D. (2001). *Dispersal*. Oxford, NY: Oxford University Press.
- Conradt, L., & Roper, T. J. (2003). Group decision-making in animals. *Nature*, 421, 155–158. <https://doi.org/10.1038/nature01294>
- Conradt, L., & Roper, T. J. (2005). Consensus decision making in animals. *Trends in Ecology & Evolution*, 20, 449–456. <https://doi.org/10.1016/j.tree.2005.05.008>
- National Research Council. (1989). *Nutrient requirements of horses*. Washington, D.C.: National Academy Press.
- Conradt, L., Krause, J., Couzin, I. D., & Roper, T. J. (2009). 'Leading according to need' in self-organizing groups. *The American Naturalist*, 173, 304–312. <https://doi.org/10.1086/596532>
- Core Team, R. (2019). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Costello, M. B. (1991). *Troop progressions of free-ranging howler monkeys (Alouatta palliata)* (Doctoral dissertation). University of California, Riverside, CA.
- Cowlishaw, G. (1996). Sexual selection and information content in gibbon song bouts. *Ethology*, 102, 272–284. <https://doi.org/10.1111/j.1439-0310.1996.tb01125.x>
- da Cunha, R. G. T., & Byrne, R. W. (2006). Roars of black howler monkeys (*Alouatta caraya*): Evidence for a function in inter-group spacing. *Behaviour*, 143, 1169–1199. <https://doi.org/10.1163/156853906778691568>
- da Cunha, R. G. T., & Jalles-Filho, E. (2007). The roaring of Southern brown howler monkeys (*Alouatta guariba clamitans*) as a mechanism of active defence of borders. *Folia Primatologica*, 78, 259–271. <https://doi.org/10.1159/000105545>
- Dasilva, G. L. (1992). The western black and white colobus as a low-energy strategist: Activity budgets, energy expenditure and energy intake. *Journal of Animal Ecology*, 61, 79–91. <https://doi.org/10.2307/5511>
- Di Bitetti, M. S., & Janson, C. H. (2000). When will the stork arrive? Patterns of birth seasonality in Neotropical primates. *American Journal of Primatology*, 50, 109–130. [https://doi.org/10.1002/\(sici\)1098-2345\(200002\)50:2<109::aid-ajp2>3.0.co;2-w](https://doi.org/10.1002/(sici)1098-2345(200002)50:2<109::aid-ajp2>3.0.co;2-w)
- Di Fiore, A., & Campbell, C. J. (2007). The atelines: Variation in ecology, behavior, and social organization. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, M. Panger & S. K. Bearder (Eds.), *Primates in perspective* (pp. 155–185). Oxford, NY: Oxford University Press.
- Dias, P. A. D., & Rangel-Negrín, A. (2015). Diets of howler monkeys. In M. Kowalewski, P. A. Garber, L. Cortés-Ortiz, B. Urbani & D. Youlatos (Eds.), *Howler monkeys: Behavior, ecology, and conservation* (pp. 21–56). New York, NY: Springer.
- Dias, P. A. D., Rangel-Negrín, A., & Canales-Espinosa, D. (2011). Effects of lactation on the time-budgets and foraging patterns of female black howlers (*Alouatta pigra*). *American Journal of Physical Anthropology*, 145, 137–146. <https://doi.org/10.1002/ajpa.21481>
- Dias, P. A. D., Coyohua-Fuentes, A., Canales-Espinosa, D., Chavira-Ramírez, D. R., & Rangel-Negrín, A. (2017). Hormonal correlates of energetic condition in mantled howler monkeys. *Hormones and Behavior*, 94, 13–20. <https://doi.org/10.1016/j.yhbeh.2017.06.003>
- Dias, P. A. D., Coyohua-Fuentes, A., Canales-Espinosa, D., Chavira-Ramírez, D. R., & Rangel-Negrín, A. (2018). Maternal condition and maternal investment during lactation in mantled howler monkeys. *American Journal of Physical Anthropology*, 167, 178–184. <https://doi.org/10.1002/ajpa.23626>
- Dingle, H. (1996). *Migration: The biology of life on the move*. Oxford, NY: Oxford University Press.
- Dufour, D. L., & Sauther, M. L. (2002). Comparative and evolutionary dimensions of the energetics of human pregnancy and lactation. *American Journal of Human Biology*, 14, 584–602. <https://doi.org/10.1002/ajhb.10071>
- Dunbar, R. I. M., & Sharman, M. (1984). Is social grooming altruistic? *Zeitschrift für Tierpsychologie*, 64, 163–173. <https://doi.org/10.1111/j.1439-0310.1984.tb00357.x>
- Emery Thompson, M. (2013). Comparative reproductive energetics of human and nonhuman primates. *Annual Review of Anthropology*, 42, 287–304. <https://doi.org/10.1146/annurev-anthro-092412-155530>
- Erhart, E. M., & Overdorff, D. J. (1999). Female coordination of group travel in wild *Propithecus* and *Eulemur*. *International Journal of Primatology*, 20, 927–940. <https://doi.org/10.1023/a:1020830703012>
- Estrada, A. (1982). Survey and census of howler monkeys (*Alouatta palliata*) in the rain forest of "Los Tuxtlas", Veracruz, México. *International Journal of Primatology*, 2, 363–372. <https://doi.org/10.1002/ajp.1350020405>
- Fernández, V. A., Kowalewski, M., & Zunino, G. E. (2013). Who is coordinating collective movements in black and gold howler monkeys? *Primates*, 54, 191–199. <https://doi.org/10.1007/s10329-013-0342-x>
- Fichtel, C., Pyritz, L., & Kappeler, P. M. (2011). Coordination of group movements in non-human primates. In M. Boos, M. Kolbe, P. M.

- Kappeler & T. Ellwart (Eds.), *Coordination in human and non-human primate groups* (pp. 37–56). Heidelberg, Germany: Springer.
- Fischhoff, I. R., Sundareshan, S. R., Cordingley, J., Larkin, H. M., Sellier, M.-J., & Rubenstein, D. I. (2007). Social relationships and reproductive state influence leadership roles in movements of plains zebra, *Equus burchellii*. *Animal Behaviour*, 73, 825–831. <https://doi.org/10.1016/j.anbehav.2006.10.012>
- Fox, J., Weisberg, S., & Price, B. (2019). Package 'car'. Retrieved from <https://cran.r-project.org/web/packages/car/car.pdf>
- Fragaszy, D. M., & Boinski, S. (1995). Patterns of individual choice and efficiency of foraging and diet in the wedge-capped capuchin, *Cebus olivaceus*. *Journal of Comparative Psychology*, 109, 339–348. <https://doi.org/10.1037//0735-7036.109.4.339>
- Furrer, R. D., Kunc, H. P., & Manser, M. B. (2012). Variable initiators of group departure in a cooperative breeder: The influence of sex, age, state and foraging success. *Animal Behaviour*, 84, 205–212. <https://doi.org/10.1016/j.anbehav.2012.04.034>
- Giraldeau, L. A., & Caraco, T. (2000). *Social foraging theory*. Princeton, NJ: Princeton University Press.
- Gittleman, J. L., & Thompson, S. D. (1988). Energy allocation in mammalian reproduction. *American Zoologist*, 28, 863–875. <https://doi.org/10.1093/icb/28.3.863>
- Glander, K. E. (1980). Reproduction and population growth in free-ranging mantled howling monkeys. *American Journal of Physical Anthropology*, 53, 25–36. <https://doi.org/10.1002/ajpa.1330530106>
- Halloy, M., & Kleiman, D. G. (1994). Acoustic structure of long calls in free-ranging groups of golden lion tamarins, *Leontopithecus rosalia*. *American Journal of Primatology*, 32, <https://doi.org/10.1002/ajp.1350320407>. 303–301.
- Harris, T. R. (2006). Within- and among-male variation in roaring by black and white colobus monkeys (*Colobus guereza*): What does it reveal about function? *Behaviour*, 143, 197–218. <https://doi.org/10.1163/156853906775900702>
- Hothorn, T., Bretz, F., & Westfall, P. (2019). Package 'multcomp'. Retrieved from <https://cran.r-project.org/web/packages/multcomp/multcomp.pdf>
- Janson, C. H., & van Schaik, C. P. (1993). Ecological risk-aversion in juvenile primates: Slow and steady wins the race. In M. E. Pereira & M. A. Fairbanks (Eds.), *Juvenile primates: life history, development, and behavior* (pp. 37–56). New York, NY: Oxford University.
- Jones, C. B. (1980). Seasonal parturition, mortality, and dispersal in the mantled howler monkey. *Alouatta palliata Gray, Brenesia*, 17, 1–10.
- Key, C., & Ross, C. (1999). Sex differences in energy expenditure in non-human primates. *Proc. Royal Soc. B*, 266, 2479–2485. <https://doi.org/10.1098/rspb.1999.0949>
- King, A. J., & Sueur, C. (2011a). Where next? Group coordination and collective decision-making by primates. *International Journal of Primatology*, 32, 1245–1267. <https://doi.org/10.1007/s10764-011-9526-7>
- King, A. J., & Sueur, C. (2011b). A rule-of-thumb based on social affiliation explains collective movements in desert baboons. *Animal Behaviour*, 82, 1337–1345. <https://doi.org/10.1016/j.anbehav.2011.09.017>
- King, A. J., Johnson, D. D. P., & van Vugt, M. (2009). The origins and evolution of leadership. *Minireview. Current Biology*, 19, 911–916. <https://doi.org/10.1016/j.cub.2009.07.027>
- Kitchen, D. M. (2004). Alpha male black howler monkey responses to loud calls: Effect of numeric odds, male companion behaviour and reproductive investment. *Animal Behaviour*, 67, 125–139. <https://doi.org/10.1016/j.anbehav.2003.03.007>
- Kitchen, D. M. (2006). Experimental test of female black howler monkey (*Alouatta pigra*) responses to loud calls from potentially infanticidal males: Effects of numeric odds, vulnerable offspring, and companion behavior. *American Journal of Physical Anthropology*, 131, 73–83. <https://doi.org/10.1002/ajpa.20392>
- Kummer, H. (1968). The coordination of travel. In D. S. Sade (Ed.), *Social organization of hamadryas baboons: A field study* (pp. 122–156). Chicago, IL: University of Chicago Press.
- Kunz, T. H., & Orrell, K. S. (2004). Energy cost of reproduction. In C. Cleveland (Ed.), *Encyclopedia of energy* (pp. 423–442). Oxford, UK: Elsevier.
- Lappan, S. (2009). The effect of lactation and infant care on adult energy budgets in wild siamangs (*Symphalangus syndactylus*). *American Journal of Physical Anthropology*, 140, 290–301. <https://doi.org/10.1002/ajpa.21069>
- Leca, J. B., Gunst, N., Thierry, B., & Petit, O. (2003). Distributed leadership in semi-free ranging white-faced capuchin monkeys. *Animal Behaviour*, 66, 1045–1052. <https://doi.org/10.1006/anbe.2003.2276>
- McCabe, G. M., & Fedigan, L. M. (2007). Effects of reproductive status on energy intake, ingestion rates, and dietary composition of female *Cebus capucinus* at Santa Rosa, Costa Rica. *International Journal of Primatology*, 28, 837–851. <https://doi.org/10.1007/s10764-007-9159-z>
- Overdorff, D. J., Erhart, E. M., & Mutschler, T. (2005). Does female dominance facilitate feeding priority in black-and-white ruffed lemurs (*Varecia variegata*) in southeastern Madagascar? *American Journal of Primatology*, 66, 7–22. <https://doi.org/10.1002/ajp.20125>
- Peng-Fei, F., Wen, X., Sheng, H., & Xue-Long, J. (2009). Singing behavior and singing functions of black-crested gibbons (*Nomascus concolor jingdongensis*) at Mt. Wuliang, Central Yunnan, China. *American Journal of Primatology*, 71, 539–547. <https://doi.org/10.1002/ajp.20686>
- Petit, O., & Bon, R. (2010). Decision-making processes: The case of collective movements. *Behavioral Processes*, 84, 635–647. <https://doi.org/10.1016/j.beproc.2010.04.009>
- Pinheiro, J., & Bates, D. (2000). *Mixed-effects models in S and S-plus*. New York, NY: Springer.
- Portman, O. W. (1970). Nutritional requirements (NRC) of nonhuman primates. In R. Harris (Ed.), *Feeding and nutrition of nonhuman primates* (pp. 87–115). New York, NY: Academic Press.
- Prins, H. H. T. (1996). *Ecology and Behaviour of the African Buffalo: Social Inequality and Decision Making*. London, UK: Chapman & Hall. <https://doi.org/10.1007/978-94-009-1527-5>
- Pyritz, L., Fichtel, C., & Kappeler, P. (2010). Conceptual and methodological issues in the comparative study of collective group movements. *Behavioural Processes*, 84, 681–684. <https://doi.org/10.1016/j.beproc.2010.02.025>
- Pyritz, L., Kappeler, P. M., & Fichtel, C. (2011). Coordination of group movements in wild red-fronted lemurs (*Eulemur rufifrons*): Processes and influence of ecological and reproductive seasonality. *International Journal of Primatology*, 32, 1325–1347. <https://doi.org/10.1007/s10764-011-9549-0>
- Pyritz, L. W., King, A. J., Sueur, C., & Fichtel, C. (2011a). Reaching a consensus: Terminology and concepts used in coordination and decision-making research. *International Journal of Primatology*, 32, 1268–1278. <https://doi.org/10.1007/s10764-011-9524-9>
- Rands, S. A., Cowlshaw, G., Pettifor, R. A., Rowcliffe, J. M., & Johnstone, R. A. (2003). Spontaneous emergence of leaders and followers in foraging pairs. *Nature*, 423, 432–434. <https://doi.org/10.1038/nature01630>
- Rhine, R. J., & Westlund, B. J. (1981). Adult male positioning in baboon progressions: Order and chaos revisited. *Folia Primatologica*, 35, 77–116. <https://doi.org/10.1159/000155968>
- Rhine, R. J., & Tilson, R. (1987). Reactions to fear as a proximate factor in the sociospatial organization of baboon progressions. *American Journal of Primatology*, 13, 119–128. <https://doi.org/10.1002/ajp.1350130203>
- Richard, A. F., Dewar, R. E., Schwartz, M., & Ratsirarson, J. (2000). Mass change, environmental variability and female fertility in wild *Propithecus verreauxi*. *Journal of Human Evolution*, 39, 381–391. <https://doi.org/10.1006/jhev.2000.0427>
- Robbins, C. T., Fortin, J. K., Rode, K. D., Farley, S. D., Shipley, L. A., & Felicetti, L. A. (2007). Optimizing protein intake as a foraging strategy to maximize mass gain in an omnivore. *Oikos*, 116, 1675–1682. <https://doi.org/10.1111/j.2007.0030-1299.16140.x>
- Robinson, J. G. (1982). Vocal systems regulating within-group spacing. In C. T. Snowdon. In C. H. Brown & M. R. Petersen (Eds.), *Primate communication* (pp. 94–116). Cambridge, NY: Cambridge University Press.
- Rodman, P. S. (1977). Feeding behaviour of orangutans of the Kutai Nature Reserve, East Kalimantan. In T. H. Clutton-Brock (Ed.), *Primate*

- Ecology (pp. 384–413). London, UK: Academic Press. <https://doi.org/10.1016/b978-0-12-176850-8.50018-4>
- Rose, L. M. (1994). Sex differences in diet and foraging behaviour in white-faced capuchins (*Cebus capucinus*). *International Journal of Primatology*, 15, 95–114. <https://doi.org/10.1007/bf02735236>
- Sekulic, R. (1982). The function of howling in red howler monkeys (*Alouatta seniculus*). *Behaviour*, 81, 38–54. <https://doi.org/10.1163/156853982x00517>
- Serio-Silva, J. C., Hernández-Salazar, L. T., & Rico-Gray, V. (1999). Nutritional composition of the diet of *Alouatta palliata mexicana* females in different reproductive states. *Zoo Biology*, 18, 507–513. [https://doi.org/10.1002/\(sici\)1098-2361\(1999\)18:6<507::aid-zoo5>3.3.co;2-i](https://doi.org/10.1002/(sici)1098-2361(1999)18:6<507::aid-zoo5>3.3.co;2-i)
- Shedden-González, A., & Rodríguez-Luna, E. (2010). Responses of a translocated howler monkey *Alouatta palliata* group to new environmental conditions. *Endangered Species Research*, 12, 25–30. <https://doi.org/10.3354/esr00287>
- Speakman, J. R. (2008). The physiological costs of reproduction in small mammals. *Philosophical Transaction of the Royal Society B: Biological Sciences*, 363, 375–398. <https://doi.org/10.1098/rstb.2007.2145>
- Steenbeek, R., Assink, P., & Wich, S. A. (1999). Tenure related changes in wild Thomas's langurs II: Long-distance calls. *Behaviour*, 136, 627–650. <https://doi.org/10.1163/156853999501496>
- Stueckle, S., & Zinner, D. (2008). To follow or not to follow: Decision making and leadership during the morning departure in chacma baboons. *Animal Behaviour*, 75, 1995–2004. <https://doi.org/10.1016/j.anbehav.2007.12.012>
- Sueur, C., Deneubourg, J. L., Petit, O., & Couzin, I. D. (2010). Differences in nutrient requirements imply a non-linear emergence of leaders in animal groups. *PLOS Computational Biology*, 6, e1000917. <https://doi.org/10.1371/journal.pcbi.1000917>
- Swingland, I. R., & Greenwood, P. J. (1983). *The ecology of animal movement*. Oxford, UK: Clarendon.
- Trillmich, J., Fichtel, C., & Kappeler, P. M. (2004). Coordination of group movements in wild Verreux's sifakas (*Propithecus verreauxi*). *Behaviour*, 141, 1103–1120. <https://doi.org/10.1163/1568539042664579>
- Turbé, A. (2006). *Foraging decisions and space use in a social mammal, the meerkat* (Unpublished doctoral dissertation). University of Cambridge, Cambridge, UK.
- Volampeno, M. S. N., Masters, J. C., & Downs, C. T. (2011). Life history traits, maternal behavior and infant development of blue-eyed black lemurs (*Eulemur flavifrons*). *American Journal of Primatology*, 73, 474–484. <https://doi.org/10.1002/ajp.20925>
- Waser, P. M. (1977). Feeding, ranging, and group size in the mangabey *Cercocebus albigena*. In T. H. Clutton-Brock (Ed.), *Primate ecology: Studies of feeding and ranging behaviour in lemurs, monkeys and apes* (pp. 183–222). London, UK: Academic Press. <https://doi.org/10.1016/b978-0-12-176850-8.50012-3>
- Waser, P. M., & Waser, M. S. (1977). Experimental studies of primate vocalisations: Specializations for long distance propagation. *Zeitschrift für Tierpsychologie*, 43, 239–263. <https://doi.org/10.1111/j.1439-0310.1977.tb00073.x>
- Watts, D. P. (1994). The influence of male mating tactics on habitat use in mountain gorillas (*Gorilla gorilla berengei*). *Primates*, 35, 35–47. <https://doi.org/10.1007/bf02381484>
- Whitehead, J. M. (1987). Vocally mediated reciprocity between neighbouring groups of mantled howling monkeys. *Alouatta palliata palliata*. *Animal Behaviour*, 35, 1615–1627. [https://doi.org/10.1016/s0003-3472\(87\)80054-4](https://doi.org/10.1016/s0003-3472(87)80054-4)
- Whitehead, J. M. (1989). The effect of the location of a simulated intruder on responses to long-distance vocalizations of mantled howling monkeys. *Alouatta palliata palliata*. *Behaviour*, 108, 73–103. <https://doi.org/10.1163/156853989x00060>
- Wright, P. C. (1984). Biparental care in *Aotus trivirgatus* and *Callicebus moloch*. In M. E. Small (Ed.), *Female primates: Studies by women primatologists* (pp. 59–75). New York, NY: Liss. [https://doi.org/10.1002/1098-2337\(1985\)11:3<262::aid-ab2480110310>3.0.co;2-n](https://doi.org/10.1002/1098-2337(1985)11:3<262::aid-ab2480110310>3.0.co;2-n)

SUPPORTING INFORMATION

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

How to cite this article: Ceccarelli E, Rangel Negrín A, Coyohua-Fuentes A, Canales-Espinosa D, Dias PAD. Sex differences in leadership during group movement in mantled howler monkeys (*Alouatta palliata*). *Am J Primatol*. 2020;e23099. <https://doi.org/10.1002/ajp.23099>