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**Vanina A. Fernández, Martín
Kowalewski & Gabriel E. Zunino**

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Who is coordinating collective movements in black and gold howler monkeys?

Vanina A. Fernández · Martín Kowalewski ·
Gabriel E. Zunino

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Abstract Decisions about when and where to travel are likely to have a strong influence on the feeding, ecology, and foraging strategies of individual primates living in a cohesive social group. Specifically, given differences in age, sex, reproductive status, or social dominance, particular group members may benefit from remaining at their present location while others may benefit from traveling to another area of their range to feed or rest. In this study, we present data on movement coordination in two groups of wild black and gold howler monkeys inhabiting Isla Brasilera (27° 20'S and 58° 40'W) in northern Argentina. We examine how factors such as sex, age, reproductive status, and dominance affect patterns of group movement coordination at feeding or resting sites, and in the context of intergroup encounters. Two groups were followed five days a month from sunrise to sunset during June to November 2004. Using focal and scan sampling techniques, we recorded 262 group displacements, the identity of the individual initiating and leading displacement, and the identity of the first individual to arrive at feeding, resting, or intergroup encounter sites. We found that overall age was the only factor that influenced group coordination: adults led more often (94.5 %) than immature individuals (5.5 %) in both groups. We did not find differences among adults. However, we found that males lead more often than females at intergroup encounters, consistent with the male-

mate defense hypothesis. The distributed leadership pattern among adults observed in this study may suggest that adult individuals make equally shared consensus decisions. This pattern should be further examined using this individual-level approach in other populations of black and gold howlers, other species of howlers, and in other atelines in which within-group social tolerance is the rule rather than the exception.

Keywords Leadership · Group coordination · Collective behavior · Decision making · *Alouatta caraya*

Introduction

Individuals that live in cohesive social units in which the group members remain in visual or auditory contact need to reach a certain level of group consensus about their displacements (Boinski 2000, Jacobs 2010). In this “consensus decision,” group members choose between two or more mutually exclusive actions with the specific aim of reaching an agreement (Conradt and Roper 2003, 2005). In this regard, a collective movement is defined by Petit and Bon (2010) as a group of animals that decide to depart or move quite synchronously, move together in the same direction (which implies that the animals have a choice between different alternatives), and maintain cohesion until the group stops moving or starts a new activity, all resulting in a change of location. It implies nonindependent individual decisions to move, and relies on information transfer between group members mediated by behavioral cues or signals, as well as social responses whose dynamics may be modulated by the ongoing collective movement itself (Petit and Bon 2010).

The participation of different individuals in the coordination of group displacements is neither random nor

V. A. Fernández (✉) · M. Kowalewski · G. E. Zunino
Estación Biológica Corrientes-Museo Argentino de Ciencias Naturales, Av. Angel Gallardo 470,
C1405DJR Buenos Aires, Argentina
e-mail: vanifer@gmail.com

G. E. Zunino
Instituto del Conurbano, Universidad Nacional de General Sarmiento, Los Polvorines, Argentina

egalitarian, and even the ability to influence the displacement decisions of a group is a reflection of the different competitive abilities and motivations of the individuals (Boinski 2000; King and Sueur 2011). Nevertheless, social processes that mediate these decisions remain unclear (Boinski and Garber 2000; Byrne 2000; Conradt and Roper 2003, 2005; King and Sueur 2011). Leaders may choose the path to follow, and this election directly influences foraging opportunities, food source selection, territory defense, and the probability of encounters with predators and conspecifics (Boinski 1991; Smith et al. 2003).

Diverse factors that are not mutually exclusive may influence social group displacements, including age, sex (reproductive status and male mate defense), and dominance relationships (see Table 1, King and Sueur 2011). There are several authors that suggest that coordination of displacement is influenced by the age of the individual (Boinski 1991; Fashing 2001a; Janson and Bitetti 1997). For example, adult members are frequently the leaders of social groups, which is probably due to their greater experience [i.e., *Saimiri oerstedii* (Boinski 1991); *Sapajus nigritus* (formerly *Cebus nigritus*) (Janson and Bitetti 1997); *Colobus guereza* (Fashing 2001a, b)].

Other studies indicate that coordination of displacement is related to the sex of the individual—for example, differences between the sexes in nutritional requirements or mating competition [*Colobus guereza* (Fashing 2001a, b); *Propithecus diadema edwardsi* and *Eulemur fulvus rufus* (Erhart and Overdorff 1999); *Papio hamadryas* (Sigg and Stolba 1981); *Saimiri oerstedii* and *Cebus capucinus* (Boinski 1991, 1993); *Hylobates lar* (Barelli et al. 2008); *Eulemur rufifrons* (Pyritz et al. 2011a)]. Wrangham (1980) suggests that while females may increase their fitness through food acquisition, males are favored if they can monopolize fertilizations. This is usually referred to as the “feeding priority” of females, assuming that females have higher energetic costs than males across certain reproductive stages (Jolly 1984; Overdorff et al. 1999; Erhart and Overdorff 1999). In this regard, it has been argued that lactating *Alouatta pigra* females consume more high-quality food than non-lactating females (Dias et al. 2011). In most studies, female coordination of feeding sites is

attributed to the greater energetic investment that females make during different reproductive states such as gestation and lactation, and/or to some specific micronutrient requirement after the weaning process (Boinski 1991, 1993; Overdorff et al. 1999; Erhart and Overdorff 1999; Pyritz et al. 2011a).

On the other hand, sex-biased coordination may be attributed to mating competition. Displacements led by males are attributed to direct or indirect mate defense (Fashing 2007). For example, in displacements toward intergroup encounters, there is evidence suggesting that when chacma baboon males (*Papio cynocephalus ursinus*) lead displacements, the opportunity for females to obtain copulations with extragroup males is reduced (Ron 1996). When resident females of *A. caraya* are receptive, resident males are more attentive and are generally first to block the access of other nonresident males to the females through mate guarding (Kowalewski and Garber 2010).

Displacements led by females have also been attributed to alternative mating strategies. A study of sociosexual strategies of the gibbon (*Hylobates lar*) suggested that nonecological factors such as mating activity may explain female leadership, and that only cycling females lead displacement more often than primary males (i.e., those that perform the majority of copulations with resident females), while there was no difference between pregnant and lactating females in this respect (Barelli et al. 2008). In this species, females who lead displacements may actively make decisions in terms of exploring their own territory and meeting neighboring groups, which makes it more likely for them to encounter potential mates. In species characterized by male leadership, females may even influence the selection of the type and quality of the food by initiating and coordinating the displacements at feeding sites (leadership at feeding contest) [*Propithecus diadema edwardsi* and *Eulemur fulvus rufus* (Erhart and Overdorff 1999); *Saimiri sp.* (Boinski 1991)].

Leadership may be also explained through the social constraints of certain primates. For example, in species with strong social dominance hierarchies, dominant individuals usually choose the displacement direction, or at the very least the decision is related to the rank of the individual (Milton 1980; Sigg and Stolba 1981; Jolly 1984; Crockett and Eisenberg 1987; Boinski 1993; Boinski and Campbell 1995; Leca 2003; Sueur and Petit 2008). This decision-making process is referred as “unshared consensus decision” (Conradt and Roper 2005, Sueur and Petit 2008, Pyritz et al. 2011b). On the other hand, species with high levels of social tolerance are reported to make equally shared decisions, which are translated into distributed leaderships, where the majority of group members could successfully lead a group movement (Conradt and Roper 2005; Sueur and Petit 2008, Pyritz et al. 2011b).

Table 1 Compositions of the study groups

Group	Adult males	Adult females	Sub-adult males	Sub-adult females	Juvenile males	Infants	Total
G	3	4 ^a	1	0	1	3 ^a	12
X	2	3	1	1	0	2 ^b	9
Total	5	7	2	1	1	5	21

^a One infant died in July 2004, and his mother died in August 2004

^b One lived for less than 24 h

The aim of this study was to explore how ecological and nonecological factors influence group coordination in black and gold howler monkeys. *Alouatta* species are distributed from 21°N to 30°S in Central and South America. The black and gold howler monkey, *Alouatta caraya*, is the southernmost of these species (Di Fiore and Campbell 2007), and its geographic range includes Paraguay, south Brazil, north and east Bolivia, and northern Argentina (Brown and Zunino 1994). *Alouatta caraya* individuals live in cohesive social groups containing 1–4 adult males, several adult females, and juveniles, and groups can have up to 21 individuals (Rumiz 1990; Bravo and Sallenave 2003; Kowalewski and Zunino 2004; Di Fiore and Campbell 2007) and present bisexual dispersal (Rumiz 1990, Oklander et al. 2010). Diets vary seasonally and are mostly composed of leaves (≈ 50 – 82 %), flowers (≈ 3 – 20 %), fruits (≈ 12 – 30 %), as well as other sources of nutrition (buds, aquatic plants ≈ 1 – 5 %) (Bravo and Sallenave 2003; Prates and Biccamarques 2008; Kowalewski 2007).

In order to explore how different factors influence group displacements in black and gold howlers, we present a set of four hypotheses. Given that black and gold howlers (1) move in cohesive units composed of individuals of different ages (Jacobs 2010), (2) present high levels of within-group social tolerance among individuals (Sueur et al. 2011), and (3) frequently show highly promiscuous intergroup encounters in both sexes at our study site (Fashing 2007; Barelli et al. 2008, Kowalewski and Garber 2010), we expected to find that: (1) adult individuals lead more often than immature individuals, as they have more experience and knowledge of the group's home range; (2) there are no differences in the frequency of group coordination among different adult individuals within the same group (distributed leadership); (3) males lead more frequently than females at intergroup encounters; and (4) adult females (in particular pregnant and/or lactating females) lead more frequently than males at feeding sites.

Methods

Study site

We conducted the study in a continuously flooded forest on Brasilera Island (27° 20'S and 58° 40'W), located near the confluence of the Paraná and Paraguay rivers in northern Argentina. The island has an area of 292 ha, and has no permanent human settlement. The climate is subtropical, with an annual average temperature of 21.7 °C and an annual average rainfall of 1247 mm (Servicio Meteorológico Nacional, 2000–2005). The island has periodic floods that result in continuous deposition of sediments and nutrients, favoring vegetation with a high rate of recovery

and a high resistance to inundation (Eskuche and Fontana 1996).

Study groups and behavioral data collection

The two neighboring study groups, G and X, had similar age and sex compositions (Table 1). An average of 70.5 % (66–77 %) of the home range of each of these groups overlapped with those of those other groups (home range of G = 5.96 ha, home range of X = 5.88 ha) (Kowalewski 2007). Both groups were habituated, and individuals were easy to identify (through ear tags, color anklets, and/or natural marks). The individuals were classified into age/sex classes following the criteria of Rumiz (1990). Although no dominance relationships could be clearly discerned among the howler males, one male had significantly closer associations with the resident females than the other males did (Kowalewski 2007). This male was defined as the “central male” (Van Belle et al. 2009). Each group was followed for five complete days per month during June to November 2004, resulting in 60 days of group data (30 days or 360 h per group).

Behavioral data were collected with the help of five field assistants (three observers per group). Two observers collected data using a focal animal sampling technique (Altmann 1974). Individual focal animals were selected randomly. When the group was traveling, the third observer registered the identity of the individual at the head of the movement. Every 10 min, this observer also performed a 2 min scan of the sample (Altmann 1974), registering sub-group size, age/sex composition, and the activities of individuals (i.e., feeding, locomotion, resting, socializing).

The scans and instantaneous focal observations allowed us to study the group behavioral contexts before and after displacements. Behavioral contexts were defined as *feeding*, *resting*, and *intergroup encounters*. We considered the group to be engaging in a certain activity if at least 50 % of all group members were involved in the activity. For this study, we considered that an intergroup encounter had occurred when two social groups came into visual contact (range 0–50 m at our study site—Kowalewski 2007).

Based on Pyritz et al. (2010) and Pyritz et al. (2011b), we constructed the following definitions to determine the behavior of individual howlers during displacements:

Initiator: an individual that begins a successful displacement.

Leader: an individual at the forefront of the displacement.

Terminator: the individual that is first to arrive at a site where the entire group remains stationary for at least 20 min.

Successful displacement: movement between two sites separated by a minimum distance of 1.5 quadrats (30 m in

a straight line) that is completed at least by 50 % of the group. In this study, we only considered successful displacements because it was difficult to register all unsuccessful attempts (individuals that attempted to start a displacement but did not recruit followers). For that reason, we have only included in our analysis displacements that we observed from beginning to end.

Successful leader: the initiator and terminator of a displacement is the same individual, sex, or age (according to which hypothesis we are testing). This individual or sex or age category was considered the successful leader of the displacement, even though there were overtakers during the displacement.

Data analysis

We used a linear mixed-effects model to analyze potential effects of age and sex on the frequency of successful displacements per individual. We performed a chi-squared test to analyze differences among individuals in the same group in terms of the frequency that each individual led a displacement. The number of adult and subadult individuals was eight in group G and seven in group X (see Table 1 for details), so we divided the number of successful displacements (initiator, terminator, and successful leader) by the number of individuals in each group. We used a parametric one-way ANOVA after verifying compliance with the assumptions of parametric statistics (using the Shapiro–Wilks and Levene tests) to analyze differences among the number of successful leader displacements per individual across different reproductive statuses. We tested the

interaction in all cases. The level of significance was set to 0.05. To perform the statistical analyses, we used InfoStat 2011 (Di Rienzo et al. 2011) and IBM SPSS Statistics 19.

Results

We registered a total of 262 successful displacements, 175 in group X and 109 in group G. The number of initiator, terminator, and successful leader displacements/individual/month was greater in group X than in group G (initiator = terminator: 0.39 ± 0.25 vs. 0.19 ± 0.13 , successful leader: 0.24 ± 0.16 vs. 0.10 ± 0.07) (Table 2). We only found age-related differences in the initiator, terminator, and successful leader frequencies (Table 2; Fig. 1). We will only consider adults hereafter because this was the category that predominantly led the displacements.

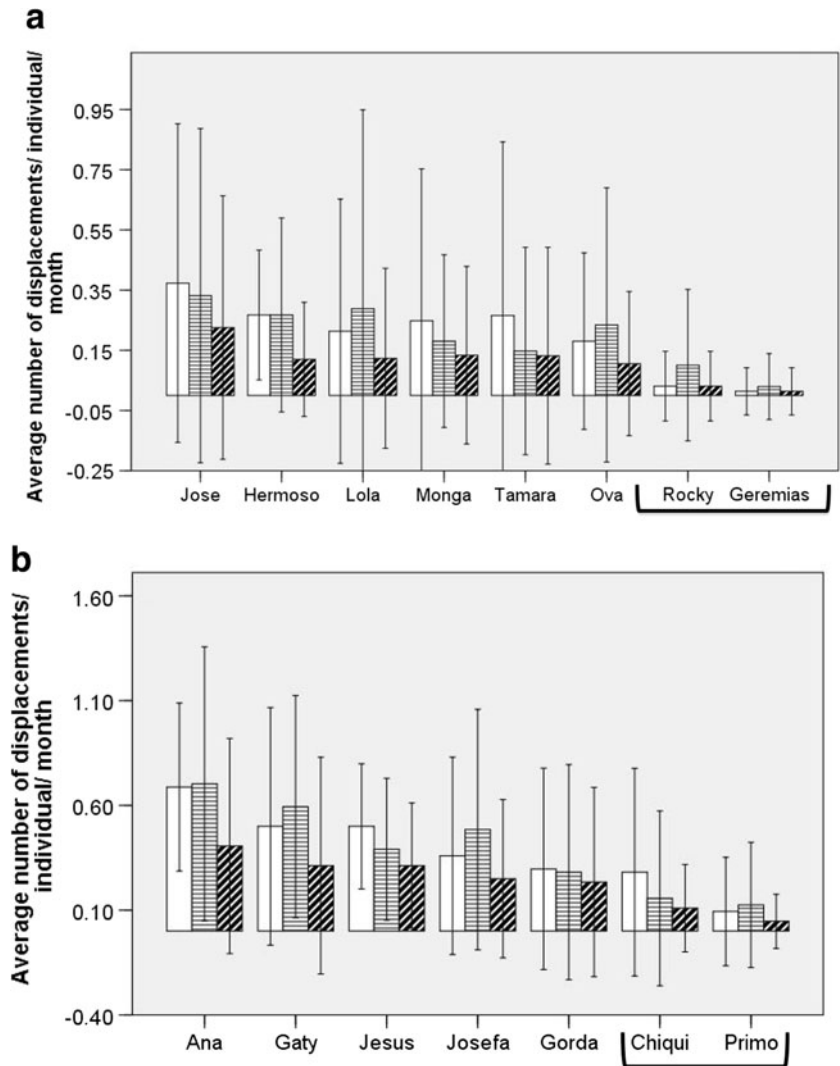
Among the adults, there were no differences in the frequency of successful leader displacement within the same group (group X: $X^2 = 7.85$, $df = 4$, $p = 0.1$; group G: $X^2 = 8.43$, $df = 5$, $p = 0.13$, Fig. 1), suggesting that all adult individuals were equally likely to lead a displacement. When we did not consider behavioral contexts, we did not find any difference between the sexes in either group in terms of the number of successful leader displacements, although group X still had a greater number of successful leader displacements than group G (Table 2). However, when we considered successful leader displacements within the different contexts, we did not find a difference between sexes at feeding and resting but we did find that males had a greater number of successful leader

Table 2 Results of LMM type III tests of fixed effects

Dependent variable	Source	Denominator <i>df</i>	<i>F</i>	<i>p</i> value
Initiator	Subject group	102.920	10.925	0.001*
	Subject sex	102.920	1.675	0.199
	Subject age	102.920	22.649	0.000*
	Interaction: sex × group	102.920	0.235	0.629
	Interaction: age × group	102.920	1.920	0.169
	Interaction: sex × age	102.920	5.892	0.017*
Terminator	Subject group	93.579	13.909	0.000*
	Subject sex	93.579	0.041	0.840
	Subject age	93.579	39.613	0.000*
	Interaction: sex × group	93.579	1.781	0.185
	Interaction: age × group	93.579	2.173	0.144
	Interaction: sex × age	93.579	0.209	0.649
Successful displacement	Subject group	104.028	6.780	0.011*
	Subject sex	104.028	0.059	0.809
	Subject age	104.028	22.573	0.000*
	Interaction: sex × group	104.028	0.000	0.989
	Interaction: age × group	104.028	1.577	0.212
	Interaction: sex × age	104.028	0.720	0.398

* *p* value < 0.05 (i.e., significant difference)

Fig. 1 Average number of displacements performed by both groups per month (**a** group G, **b** group X). Immature individuals are *underlined*. Error bars ± 2 SD. White bars show initiators, white striped bars show terminators, while black striped bars show successful leaders



displacements at intergroup encounters in both groups (Table 3; Fig. 2).

Finally, in this study we examined the frequency of successful leader displacements by females at different reproductive stages (Table 4). In contrast to what was expected, we observed no difference between the feeding site displacements led by lactating (Fl) and non-lactating females [non-pregnant and non-lactating females (Fnpl) + pregnant females (Fp)] (ANOVA, $F = 0.02$, $df = 1$, $p = 0.90$), although the number of individuals in each category was low.

Discussion

In this study, we tested a set of hypotheses in order to determine how different factors can influence group displacements in black and gold howlers. In concordance with our predictions, we found that mature individuals led more

frequently than immature individuals (94.5 % vs. 5.5 %). These results agree with reports of adults leading displacements in other primates (Boinski 1991; Janson and Di Bittetti 1997; Fashing 2001a, b; Barelli et al. 2008). Adult leadership in primate groups is often attributed to the fact that immature individuals lack experience and knowledge of the home range (Janson and van Schaik 1993). Black and gold howler monkeys do not move randomly in their home range (Fernández, unpublished data), and the fact that adult individuals lead the movements could be related to spatial knowledge that they may have of the home range.

As we expected, we did not find differences among adult individuals in any of the groups. This is referred to as “distributed leadership,” and is a clearly pattern that we observed at group level (Pyritz et al. 2011b). Species with high levels of social tolerance are reported to share decision-making equally, which translates into distributed leadership (Conradt and Roper 2005; Sueur and Petit 2008; Pyritz et al. 2011b). This was an expected pattern for

Table 3 Successful leader displacements within different behavioral contexts (feeding, intergroup encounters, and resting) in both groups

Dependent variable	Source	Denominator <i>df</i>	<i>F</i>	<i>p</i> value
Feeding	Sex	71.133	0.939	0.336
	Group	71.133	10.943	0.001*
	Interaction: sex × group	71.133	0.220	0.641
Encounter	Sex	45.753	20.154	0.000*
	Group	45.753	8.764	0.005*
	Interaction: sex × group	45.753	2.626	0.112
Resting	Sex	61.857	1.747	0.191
	Group	61.857	11.030	0.002*
	Interaction: sex × group	61.857	0.348	0.557

Results of LMM type III tests of fixed effects are shown.

* *p* value <0.05 (i.e., significant difference)

Fig. 2 Successful leader displacements at different behavioral contexts (feeding, intergroup encounters, and resting). Group X had a greater number of successful leader displacements than group G. There was only a difference between the sexes during intergroup encounters: males had a greater number of successful leader displacements than females in both groups. Error bars ±2 SD, *p* value <0.05

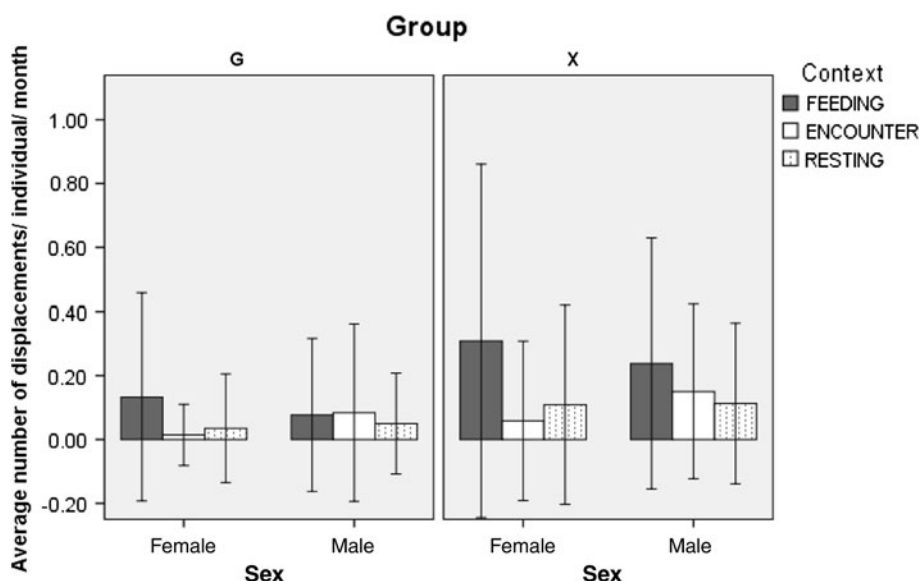


Table 4 Reproductive states of females in group X and group G during the study

Group	X			G			
	Female 1	Female 2	Female 3	Female 4	Female 5	Female 6	Female 7
Month (all in 2004)							
April	G	G	PR	G	G	L2	G
May	L	L	G	L	G	L2	L
June	L	L	G	L	L	L2	L
July	L	L	G	L	Infant dead	PR	L
August	L	L	G	L	Female dead	PR	L
September	L	L	Birth (dead)	L		PR	L
October	L	L	PR	L2		PR	L
November	L2	L2	PR	L2		PR	L2

The first column indicates the month during 2004. PR potentially reproductive, G gestation, L in the first six months of lactation, L2 in months 7–9 of lactation (extracted from Kowalewski 2007)

A. caraya due to the complete or almost complete lack of social dominance hierarchy in this species (Kowalewski 2007; see also Bezanson et al. 2008: *Alouatta palliata*; Wang and Milton 2003: *Alouatta palliata*). However, in our study, we were not able to discern whether this group-level pattern is a consequence of equally shared decisions or an individual-level process (Sueur and Petit 2008; King and Sueur 2011; Pyritz et al. 2011b).

In our study, we expected a sex-biased pattern attributable to mating competition (male leadership) and feeding priorities (female leadership), but females and males were just as likely to lead displacements (probability: males 48.1 %, females 51.9 %). However, when we considered the behavioral context (feeding, resting, and intergroup encounters), a sex-biased pattern did emerge, but only for males. The absence of a difference between males and

females in terms of leadership toward feeding sites is possibly related to the fact that males are just as interested in reaching feeding sites as females are, or that they have similar energetic requirements. Several authors have suggested that, in black and white colobus (*Colobus guereza*) groups, males may defend food resources as a form of indirect mate defense (Fashing 2001a, b, 2007; Harris 2006; Sicotte and MacIntosh 2004). In this sense, females would prefer males that are successful in food defense as mating partners. At this moment, we lack any evidence to reject this hypothesis.

Females were expected to lead displacements more frequently towards feeding contexts than resting or intergroup encounters, due to the greater energetic investment that females make during lactation (Boinski 1991, 1993; Overdorff et al. 1999; Erhart and Overdorff 1999; Dias et al. 2011). However, in contrast to the results of studies of *S. oerstedii* (Boinski 1991), *P. diademata edwardsi*, *E. fulvus rufus* (Overdorff et al. 1999; Erhart and Overdorff 1999), and *Eulemur rufifrons* (Pyritz et al. 2011a), we did not find that females led the groups towards feeding sites more than males did. Moreover, we expected to find that lactating females, due to their extra energetic requirements, would lead displacements towards food more often than non-lactating females, but this was not observed.

There are several potential explanations for the observed lack of this pattern. Females across different reproductive states do not have high energetic food-related constraints throughout the year. Kowalewski and Zunino (2004) suggested that howler monkeys at our study site do not have a fixed birth season, which is possibly related to a high, uniform, and relatively predictable levels of food available throughout the year. On the other hand, females across different reproductive states may have similar energetic constraints to females during gestation or those with dependent infants. Pyritz et al. (2011a), in a study on displacement of *Eulemur rufifrons* in Madagascar, suggested that female leadership occurs year-round, independent of reproductive seasonal patterns, indicating that females may continue to initiate and lead group movements between the weaning of an infant and the next mating season. Increasing the number of females studied at sites with different food availability characteristics may shed light on these findings in the future.

We found that males lead more often than females at intergroup encounters. At our study site, Kowalewski (2007) suggested that there was a pattern of increased use of overlapping quadrants and increased frequency of intergroup encounters during periods when females in neighboring groups were more receptive. Also, males in both groups were more attentive and were generally the first to block the access of other resident or nonresident

males to females during fertile periods through mate guarding (Kowalewski and Garber 2010; see also Ron 1996: *Papio cynocephalus ursinus*). In addition, the 53.4 % of the extragroup copulations occurred during frequent intergroup encounters (1 encounter per 4.7 observation hours) (Garber and Kowalewski 2011). Females of *A. caraya* are characterized by promiscuous within- and between-group mating patterns in which females copulate with intra- and extragroup males during breeding and nonbreeding periods (Kowalewski and Garber 2010). The positive association between the use of overlapping quadrants within the home range and the frequency of intergroup encounters when females were more receptive is more consistent with the male-mate defense hypothesis.

In summary, our results indicate that group coordination of displacements in these two groups of *A. caraya* depends on the age of the individual: adult individuals are usually the leaders of group progressions. At our study site, there did not seem to be a sex-related pattern associated with a special need for food acquisition in females, as both sexes were equally likely to lead the progression, as were females of different reproductive statuses. However, males tended to lead at intergroup encounters, which may be consistent with the male-mate defense hypothesis. These results show the importance of breaking down analyses of displacement according to behavioral context (i.e., feeding sessions, resting sessions, and intergroup encounters) in order to look for particular hidden patterns.

Finally, the fact that we found a distributed leadership pattern may suggest that adult individuals make equally shared consensus decisions. For many group members, equally shared decisions result in lower consensus costs than unshared decisions (Conradt and Roper 2003). Howlers are characterized by low levels of within-group aggression and high levels of within-group social tolerance, so we might expect to find consensus decisions in groups of howlers more often than not. This pattern should be examined further using this individual-level approach in other populations of black and gold howlers, other species of howlers, and in other atelines that display within-group social tolerance.

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