Female Participation in Collective Group Defense in Black Howler Monkeys (Alouatta pigra)

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Many group-living animals actively defend a home range against neighboring groups. In many of these societies, males are the primary participants during group defense, while female participation ranges from seldom to frequent. Among howler monkeys (Alouatta spp.), loud calls (i.e., howling) are often used in the context of intergroup spacing as a form of cooperative group defense. Males initiate and lead these howling bouts, but females occasionally participate as well. During a 28-month study, I examined social and ecological factors influencing the participation of adult females in naturally occurring howling bouts of five multimale–multifemale groups of black howler monkeys (A. pigra) at Palenque National Park, Mexico. I calculated the percentage of time each female participated during howling bouts for which the participation of all resident females could be recorded /C21/80% of the time (N = 287). At least one female was observed to participate in 53% of the vocal displays. Female participation was significantly greater during howling bouts that were part of visual intergroup encounters compared to spontaneous calls or calls in response to nearby calls when there was no visual contact with rival groups. Female calling behavior was not influenced by the presence of infants vulnerable to infanticide or by the proximity to food resources. Nonetheless, in four of the five study groups, one female called significantly more than the other resident female(s), suggesting that these females played a special role within the group’s social dynamics, not previously recognized for this species. Am. J. Primatol. 77:595–604, 2015.

Key words: Alouatta pigra; black howler monkey; collective action; group defense; loud calls; female behavior

INTRODUCTION

Group living requires that individuals form predictable social relationships, share common resources, and develop cooperative alliances to defend resources against other groups [Nunn, 2000; Sussman & Garber, 2011; van Schaik, 1983]. In many group-living societies, males participate more frequently in group defense than females [Kitchen & Beehner, 2007]. Female participation may range from seldom (e.g., white-faced capuchins, Cebus capucinus [Perry, 1996]; mountain gorillas, Gorilla beringei [Robbins & Sawyer, 2007]), to occasionally (e.g., guereza monkeys, Colobus guereza [Fashing, 2001]; Japanese macaques, Macaca fuscata [Majolo et al., 2005]; meerkats, Suricata suricatta [Mares et al., 2012]), to being similar to males (e.g., lions, Panthera leo [McComb et al., 1994]; coyotes, Canis latrans [Gese, 2001]; black-tufted-ear marmosets, Callithrix penicillata [Decanini & Macedo, 2008]), to females being the primary participants instead of males (e.g., diana monkeys, Cercopithecus diana [Hill, 1994]; spotted hyenas, Crocuta crocuta [Boydston et al., 2001]; blue monkeys, Cercopithecus mitis [Cords, 2007; Payne et al., 2003]). Because female fitness is most likely limited by access to food resources [Trivers, 1972], female participation in group defense is hypothesized to principally involve the defense of food resources (e.g., Tana river mangabeys, Cercocebus galeritus [Kinnaird, 1992]; western black-and-white colobus monkeys, Colobus polykomos [Korstjens et al., 2005]) or the defense of vulnerable infants in infanticidal species (e.g., lions, [Packer et al., 2001; Spong & Creel, 2004].

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Conversely, male fitness is hypothesized to be most likely limited by access to fertile females such that their participation in group defense mainly involves mate defense [Trivers, 1972]. Males may accomplish this by either directly defending access to resident females, by defending resources that resident females need to successfully reproduce, or by defending infants in infanticidal species [Cheney, 1987; Fashing, 2001]. Males, however, may act as “hired guns” [sensu Rubenstein, 1986] for females when their direct mate defense efforts also exclude food competitors or infanticidal males.

In addition to potential differences in group defense strategies between males and females, individual females may vary in their participation in collective group defense based on the cost-benefit trade-offs associated with group defense [Kitchen & Beehner, 2007; Mares et al., 2012; Nunn & Lewis, 2001]. For example, higher ranking females, who are likely to accrue greater benefits (through their priority of access to food resources) or to incur lower costs (through their better physical conditions), have been observed to provide group defense more frequently than lower ranking females in coyotes [Gese, 2001], ring-tailed lemurs, Lemur catta [Nunn & Deaner, 2004], and blue monkeys [Cords, 2007]. In addition, the presence of infants could also influence individual female’s participation in group defense because females with infants are most likely to bear higher costs (risk of injury or death of infant) than females without infants [Cords, 2007]. However, in species in which infanticide by extragroup males is an imminent threat, females with unweaned infants might accrue higher benefits, relative to costs, when their participation influences the balance of power between opposing groups [Kitchen, 2006].

In the present study, I examine social and ecological factors that promote female participation in naturally occurring loud calls and intergroup encounters in black howler monkeys (Alouatta pigra). Howler loud calls (i.e., howling) include roars and barks, which are amplified in the enlarged hyoid bone of males [Schön, 1971; Schön Ybarra, 1986], are often used in the context of intergroup spacing as a form of cooperative group defense [da Cunha & Byrne, 2006; Holzmann et al., 2012; Hopkins, 2013; Van Belle et al., 2013a, 2014a]. Howler monkeys may howl either spontaneously without a discernible external stimulus, in response to nearby howling emitted by neighboring groups that are outside sighting distance, or during visual encounters with neighboring groups or non-group individuals [Holzmann et al., 2012; Sekulic, 1982; Van Belle et al., 2013a; Whitehead, 1987]. Males initiate and lead howling bouts, but females have been observed to join males during vocal displays [Baldwin & Baldwin, 1976; Chiarello, 1995; Holzmann et al., 2012; Kitchen, 2006; Sekulic, 1983]. Females are equipped with a less enlarged hyoid bone compared to males resulting in roars and barks that are aurally distinct from those produced by males [Sekulic, 1983; Whitehead, 1989]. The time and energy that females (as well as males) invest in calling is assumed to be costly given the vigorous behavioral displays during howling bouts compared to an otherwise energy-minimizing lifestyle.

The majority of howling bouts produced by black howler monkeys are spontaneous (33%), response (29%), and intergroup encounter calls (33%) [Van Belle et al., 2014a]. These calls disproportionally occur in a feeding context and are concentrated in areas in the home range that contain major feeding sites, suggesting that loud calling in howler monkeys most frequently function in food defense [Van Belle et al., 2014a see also Chiarello, 1995; Hopkins, 2013; Sekulic, 1982; Whitehead, 1987]. It is hypothesized that loud calls function in resource defense through advertising group members’ fighting ability or motivation to escalate contests [Chiarello, 1995; Sekulic & Chivers, 1986; Van Belle et al., 2014a]. Females might be motivated to join males in vocal displays if their participation influences the outcome of intergroup contests over feeding sites. Indeed, during playback experiments in mantled howler monkeys (A. palliata), groups were more likely to retreat when they were broadcast recordings that included both male and female calls compared to recordings of only male calls [Whitehead, 1989]. During spontaneous or response calls when they have no visual contact with opponents, the threat of losing access to nearby food resources to neighboring groups is less immediate, and females might reduce their participation and rely more on male group defense efforts.

Black howler females do not always participate in unison during howling bouts [Kitchen, 2006], suggesting that individual females might adopt different strategies during group defense. During playback experiments that simulated the intrusion of unfamiliar males, nevertheless, the presence of infants did not influence the howling behavior of individual females [Kitchen, 2006], despite the fact that non-group males may attempt to take over the group, evict resident males, and commit infanticide [Crockett, 2003; Van Belle et al., 2010]. Female participation in naturally occurring howling bouts across these different contexts, however, has not been investigated in black howler monkeys.

In this paper, I present data on female participation in naturally occurring loud calls collected during a 28-month study of five multimale–multifemale black howler groups in Palenque National Park, Mexico. I predict that (i) if female participation is influenced by the presence of infants, then females should participate more (or less) when they have infants vulnerable to infanticide compared to when they have no infants; (ii) if female participation in howling bouts serves in the defense of important food
resources, then females should participate more frequently when they are in the immediate vicinity of important food resources than when no food resources are near; and (iii) if the immediacy of threat posed by opponents influences female participation, then females should increase their participation in howling bouts during encounters with opponents with whom they have direct visual contact compared to opponents with whom they have no visual contact. These predictions are not mutually exclusive.

METHODS

Study Site and Subjects

Palenque National Park (PNP), Mexico (17° 28′ N, 92° 03′ W) encompasses an area of 1,771 ha of which approximately 1,000 ha contain primary and secondary tall evergreen tropical rainforest. The remaining area consists of pasture [Díaz Gallegos, 1996]. I selected three multimale–multifemale black howler groups (Balam, Pakal, and Motiepa) for systematic observations during an initial study period (September 1, 2010–December 11, 2011). I observed two different neighboring groups (Bolas and Unites) during a second study period (March 1, 2012–February 12, 2013). The Balam, Bolas, and Pakal groups had two (LU and TE), three (AO, DK, and PM), and three (ES, PR, and PU) adult females, respectively, throughout their corresponding study period. The Unites group had three adult females (GA, MN, and LL) at the onset of their study period, but one female (MN) disappeared 5 months into the observation period (July 20, 2012). For some analyses, data from the Unites group were separated in before and after the female disappeared. The Motiepa group had two adult females (ML and IS) at the onset of their study period, but one female (IS) disappeared during the second to last month of observations (November 3, 2011). Only data collected when both females were present in the Motiepa group were considered in the analyses.

The research complied with protocols of the Animal Care Committee of Universidad Nacional Autónoma de México and adhered to the legal requirements of Mexico and the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates.

Data Collection

During each study period, I observed the respective study groups for two blocks of three consecutive days (approx. 0530–1700 hr) per month, resulting in 383 observation days and 3,964 observation hours (Table I). I conducted instantaneous scan samples [Altmann, 1974] at 15 min intervals to record the behavior of all visible group members. Behaviors were classified into resting, feeding, moving (i.e., within the same feeding or resting site), traveling (i.e., collective group movement to distant feeding or resting sites), vocalization, and social behavior. When an individual was observed feeding, I also recorded the food item (i.e., young or mature leaves, ripe or unripe fruits, stems, or flowers).

In addition, during each scan sample, I recorded the geographic coordinates of the group’s estimated center of mass using a Garmin E-Trex Venture GPS unit (Garmin International, Olathe, Kansas, USA; mean satellite accuracy = 7.7 m).

I collected data on howling bouts (i.e., a combination of roaring and barking by one or more group members) using all-occurrence sampling [Altmann, 1974]. For each howling bout, I recorded the start and end time, the geographic coordinates of the howling location, and the behavioral context (i.e., resting, feeding, or traveling) in which the howling occurred. For each behavioral context, 75% of the visible independently moving group members had to engage in the activity immediately prior to the onset of the howling bout. In addition, I recorded whether howling was (i) spontaneous (i.e., no discernible external stimulus), (ii) in response to nearby howling without visual contact with the caller(s), (ii) as part of an encounter with a neighboring group, or (iv) during an encounter with non-group individuals (i.e., solitary males or females, or pairs that do not belong to an established group). I considered howling to be a response call whenever a nearby howling bout, estimated at >50–300 m, had begun prior to and was ongoing during the start of the focal group’s loud calling [Van Belle et al., 2013a; Whitehead, 1987]. I scored encounters whenever a neighboring group or non-group individual(s) were within 50 m of the focal group (i.e., visual contact) [Hopkins, 2013; Van Belle et al., 2013a]. For each howling bout, I also recorded, whenever possible, the participation by each adult female via instantaneous scan samples at 1-min intervals relative to the onset of the howling bout. A female was considered to participate whenever she was observed to howl, be vigilant, break or shake branches, and/or display pilo-erection (the latter four behaviors were occasionally observed during inter-group encounter calls). I considered two howling bouts to be independent when all group members were silent for at least 10 min in between howling bouts [Holzmann et al., 2012; Hopkins, 2013; Van Belle et al., 2013a].

Data Analyses

It was not always feasible to record the participation of each resident adult female throughout the
entire bout because they sometimes moved out of view for periods of time. Therefore, I calculated per howling bout for each female the percentage of scans during which her participation (i.e., yes or no) could not be recorded out of all scans collected throughout the bout. I excluded from the analyses those bouts for which the participation of at least one resident female was unknown for more than 20% of the scans. In addition, because sample size of female participation in howling bouts during encounters with non-group individuals was small (mean = 2.8 ± SD 1.6 bouts/group, range = 1–5 bouts/group, N = 14), these data were excluded from the analyses. Given that I was more successful in the field in recording the participation of all resident females when they did not join the resident male(s) during the howling bout, bouts in which only males howled were overrepresented in the dataset. To avoid underestimating female participation, I first calculated for each group the percentage of bouts in which females participated out of all bouts recorded (considering only spontaneous, response, and intergroup encounter calls) for which I knew whether females participated or not (without considering further details on female identities or duration of their participation). I then eliminated from the dataset for which sufficient information on female participation was collected (as explained above) randomly selected howling bouts (N = 9–13 per group) in which only resident males participated such that the percentage of bouts in which females participated computed for the dataset to be analyzed was virtually equal to that computed for the complete dataset. In total, I analyzed 287 howling bouts (47% of all recorded howling bouts, Table I). The mean duration for these howling bouts was 13.7 ± SE 0.6 min (median = 10.8 min, range = 13 s–108 min). For each of these howling bouts, I calculated the percentage of scans each female participated out of all scans her participation was known.

To examine whether female participation was influenced by social and ecological factors, I conducted two separate generalized linear mixed models (GLMM). The response variable of the first GLMM (with a binomial error structure and a logit link function) indicated per howling bout whether females participated (i.e., yes or no), while that of the second GLMM (with a Gaussian error structure) represented per bout the mean of the percentages of scans resident females participated averaged across the resident females. For the latter, only those bouts during which at least one female participated were included in the model. In both models, group identity was included as a random variable. The predictor variables (with fixed effects) included howling context (i.e., spontaneous, response, or intergroup encounter calls), the presence (i.e., yes or no) of infants vulnerable to infanticide (estimated to be younger than nine months of age [Crockett, 2003]), and the percentage of feeding records in the vicinity of the howling location. I calculated these percentages of feeding in the howling vicinity by drawing a circle of 28 m around each howling location using Arcview 3.2 (ESRI, Redlands, California, USA). I chose a radius of 28 m because the area of each circle was virtually equivalent to the area encompassed by 50 × 50 m quadrats, which have been used in previous studies [e.g., da Cunha & Byrne 2006; Fashing, 2001; Harris, 2006]. For each bout, I computed the percentage of time group members fed within a 28 m radius from the howling location out of all feeding records collected that day. These feeding percentages, as well as the mean of the percentage of scans females participated in the second GLMM model, were square-root transformed to conform to a normal distribution (Kolmogorov–Smirnov tests: P > 0.05). In addition, I conducted Fisher exact tests to examine whether female participation in howling bouts was influenced by the behavioral context (i.e., feeding, resting, or traveling), in general, or the feeding context (i.e., young or mature leaves, ripe or unripe fruits, stems, or flowers), in particular, in which the howling occurred.

To assess whether resident females differed in the mean percentage of scans they participated during howling bouts, I used paired permutation tests for each intragroup female dyad given that their participation was collected simultaneously. To

### Table I. Number of Observation Days and Contact Hours per Study Group, as Well as Number of Howling Bouts Included in the Analyses per Howling Context and per Group

<table>
<thead>
<tr>
<th>Group</th>
<th>Observation days</th>
<th>Contact hours</th>
<th>Number of howling bouts</th>
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<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Spont</td>
</tr>
<tr>
<td>Balam</td>
<td>81</td>
<td>827</td>
<td>24</td>
</tr>
<tr>
<td>Bolas</td>
<td>76</td>
<td>790</td>
<td>19</td>
</tr>
<tr>
<td>Motiepa</td>
<td>74</td>
<td>769</td>
<td>21</td>
</tr>
<tr>
<td>Pakal</td>
<td>75</td>
<td>762</td>
<td>24</td>
</tr>
<tr>
<td>Unites</td>
<td>77</td>
<td>816</td>
<td>9</td>
</tr>
<tr>
<td>Sum</td>
<td>383</td>
<td>3964</td>
<td>97</td>
</tr>
</tbody>
</table>

*Note: Spont, spontaneous calls; Response, response calls; IGE, intergroup encounter calls.*
further assess which factors influenced individual female participation, I calculated per female the mean percentage of scans in which she participated (i) for spontaneous, response, and intergroup encounter calls separately, and (ii) for the period when she had a vulnerable infant versus the period when she did not (irrespective of howling context). I then used paired t-tests to assess whether females participated differently across the three howling contexts (N = 13 females) or when they had vulnerable infants or not (N = 10 females). Three females (GA, TE, and MN) did not have vulnerable infants throughout the study period.

Statistical analyses were performed in R 3.0.2 [R Core Team, 2013]. I used the glmer and lmer functions from the lme4 package [Bates et al., 2013] for the GLMMs with binomial and Gaussian error structure, respectively. Because the lmer function does not provide P-values, I derived these using the lmerTest package [Kuznetsova et al., 2013]. All tests were two-tailed, and the alpha level was set at 0.05.

RESULTS

At least one female participated in 153 of the 287 (53.3%) howling bouts (Table II). Of these, only one resident female participated in 66 (43.1%) bouts, while two or three resident females participated in 87 (56.9%) bouts (Table II). All resident females present in the group were observed to participate together in (56.9%) bouts (Table II). All resident females present in the group were observed to participate together in (56.9%) bouts (Table II). All resident females present in the group were observed to participate together in (56.9%) bouts (Table II). All resident females present in the group were observed to participate together in (56.9%) bouts (Table II). All resident females present in the group were observed to participate together in (56.9%) bouts (Table II).

When I considered the mean of the percentage of scans resident females howled during these bouts when at least one female participated similar results were obtained. Mean female participation during bouts was influenced by howling context (IGE versus spontaneous calls: GLMM estimate = 2.25 ± SE 0.43, t147.9 = 5.2, P < 0.0001; IGE versus response calls: estimate = 1.66 ± SE 0.40, t143.5 = 4.2, P < 0.0001), but not by the presence of vulnerable infants (estimate = −0.20 ± SE 0.37, t135.7 = −0.5, P = 0.589) or the feeding percentage in the vicinity of the howling location (estimate = −0.09 ± SE 0.08, t147.4 = −1.1, P = 0.264).

Females did not join howling bouts more or less frequently when they were resting (mean = 44.3 ± SE

<table>
<thead>
<tr>
<th>TABLE II. Percentages of Howling Bouts per Study Group in Which One, Two, or Three Resident Adult Females (AF) Participated</th>
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<tr>
<td>Group</td>
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<tr>
<td>-------</td>
</tr>
<tr>
<td>Balam</td>
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<tr>
<td>Belas</td>
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<tr>
<td>Motiepa</td>
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<tr>
<td>Pakal</td>
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<tr>
<td>Unites 1</td>
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<td>Unites 2</td>
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Note: Unites 1 and 2 represent the observation period before and after the adult female MN disappeared on July 20, 2012.

Fig. 1. Mean ± SE howling bout duration (min) in which females participated or not across different howling contexts: spontaneous calls (Spont), response calls (Response), and intergroup encounter calls (IGE). The means were calculated from the means per study group.
6.5% of bouts, averaged across study groups; Fisher exact test: $P = 0.177, N = 121$), traveling (mean = 61.7 ± SE 9.7% of bouts; $P = 0.151, N = 35$), or feeding (mean = 58.3 ± SE 5.8% of bouts; $P = 0.181, N = 131$). Additionally, females were not more or less likely to participate in howling bouts when they were feeding on young leaves (mean = 54.1 ± SE 9.2% of bouts; $P = 0.627, N = 24$) or unripe fruits (mean = 56.3 ± SE 17.0% of bouts; $P = 0.201, N = 20$). There was a tendency for females to participate more when they were feeding on ripe fruits (mean = 61.0 ± SE 12.0% of bouts; $P = 0.072, N = 57$), but this result did not reach statistical significance. No tests could be conducted on female participation in bouts when they were feeding on mature leaves, stems, or flowers because of small sample sizes ($N = 3, 15, 4$ bouts, respectively).

Individual females participated in 18.5–57.8% (mean = 36.0 ± SE 3.8%) of howling bouts. The mean percentage of scans within bouts that individual females participated ranged between 9.7 and 28.4% of scans (Fig. 2). For four study groups, resident females differed significantly in their percentage of time they participated during howling bouts, with one female contributing significantly more than the other resident females (Fig. 2). In the Unites group, the two or three resident females participated similarly during howling bouts (Fig. 2).

Individual females participated more frequently during intergroup encounters calls than during spontaneous and response calls (paired $t$-tests: IGE versus spontaneous calls: $t = 6.7, P < 0.001$; IGE versus response calls: $t = 5.6, P < 0.001, N = 13$ females, Fig. 3). Females participated at similar rates when they had vulnerable infants as when they did not (paired $t$-test: $t = 0.6, P = 0.543, N = 10$ females, Fig. 4).

**DISCUSSION**

Based on a detailed study of female howling behavior across different social and ecological contexts in five neighboring groups of *A. pigra*, I found that females participated in more than half (53%) of the howling bouts, considerably more frequently than reported in previous howler monkey studies (*A. guariba*: 28% of 46 calls [Chiarello, 1995]; *A. pigra*: 47% of 131 intergroup encounter calls [Kitchen, 2006]; sympatric *A. guariba* and *A. caraya* combined: 29% of 23 calls [Holzmann et al., 2012]). These differences could reflect variation among species, in the main function of loud calls among different populations [da Cunha & Byrne, 2006; Holzmann et al., 2012; Van Belle et al., 2014a], in the proximate mechanisms with which home ranges are defended (e.g., vocal border patrol versus regular advertisement of occupancy of entire home range [da Cunha & Byrne, 2006; da Cunha & Jalles-Filho, 2007; Van Belle et al., 2013a], or in the level of between-group competition among different populations (related to population density and food availability), and thus in the variation of both male and female strategies during group defense. More studies are needed to understand variation in female calling behavior among distinct howler species and populations.

Even though infanticide in black howler monkeys has been observed after non-group males took over social groups [Van Belle et al., 2010 see also Brockett et al., 1999] and males engaged in more vigorous vocal

![Bar chart](image.png)

Fig. 2. Mean ± SE percentage of scans in which each female participated during howling bouts. Statistical differences within each group, assessed with paired permutation tests, are indicated with the letters a and b.
displays during playback experiments when vulnerable infants were present in their group than when not [Kitchen, 2004], females were not observed to alter their participation in howling bouts when they had dependent infants. This could result from the fact that the analyses only included spontaneous, response, and intergroup encounter calls, when the risk of infanticide is minimal. The low rate at which non-group males were encountered by the study groups (one encounter every 200 observation hours [Van Belle et al., 2014a]), along with the need for detailed information on female participation, impeded statistical analyses. Still, during playback experiments that simulated the intrusion of unfamiliar males in another population, black howler females with small offspring were equally likely to join males during vocal displays as females without small offspring [Kitchen, 2006]. The findings of both studies indicate that infant defense is not the primary reason for individual female participation in loud calls in this species.

Nevertheless, females living in groups that had no dependent infants tended to approach the speakers more closely during playback experiments during Kitchen’s study [Kitchen, 2006]. A similar, but also statistically insignificant, trend was observed during this study in that at least one female howled in a higher percentage of bouts when no infants were present in the group (57.5%) than when at least one infant was present (50.5%). Kitchen [2006] suggested that if females co-reside with female relatives, as was
observed in four of the five study groups [Van Belle et al., 2014b], a female might accrue inclusive fitness by engaging in infant defense efforts when female companions have vulnerable infants even if she does not have infants on her own. However, it seems that black howler females rather reduced their contribution to group defense when infants were present, and thus inclusive fitness gains might not play an important role in female group defense strategies.

The regular participation by females in howling bouts suggests that female calling behavior mainly functions to defend food resources, particularly because howling bouts in general occurred disproportionally in feeding contexts, especially when feeding on ripe fruits, and were concentrated in areas in the home range that contained major feeding sites [Van Belle et al., 2014a]. However, this hypothesis did not receive further support as females were not more likely to participate in or participate for longer during howling bouts that were in the immediate vicinity of food resources consumed that day or that occurred in a feeding context. This suggests that female participation in group defense is not strictly correlated to the defense of food resources in this species. Similarly, in guerezas, females’ occasional participation during intergroup encounters was not correlated to feeding rates in the area of the encounter location, contrasting with the positive correlation between levels of male aggression during intergroup encounters and feeding rates close by [Fashing, 2001]. In the absence of evidence that females defended infants, Fashing [2001] still invoked the female resource defense hypothesis as the most likely explanation of female behavior during intergroup encounters in guerezas [Fashing, 2001; see also Harris 2006, 2010].

In a closely related colobus species, the western black-and-white colobus, females participated more regularly during intergroup encounters than guereza females [Korstjens et al., 2005]. Also for this species, the proportion of intergroup encounters that involved female aggression was not associated with the frequency with which the group fed in the quadrant where the encounter occurred, nor with the percentage of fruit in the diet [Korstjens et al., 2005]. Nevertheless, females’ level of intergroup aggression was most elevated when one particularly important food resource, fruits from Pentaclethra macrophylla, was temporarily available, suggesting that the defense of food played a major role in female group defense strategies [Korstjens et al., 2005]. Black howler female participation in howling bouts may also be associated with phenological patterns of particular fruit resources, especially given that there was a tendency for females to participate in more howling bouts when ripe fruits were at stake. Assessing female calling behavior relative to temporal and spatial food availability of important food resources, as well as food patch size, quality, and quantity, might further elucidate the role loud calls play in food resource defense in black howler monkeys.

In ursine howler monkeys (Alouatta arctoidea), female participation in vocal displays is hypothesized to stimulate male calls based on observations that males vocalized more in response to recordings of only female calls compared to recordings of only male calls or male and female calls [Sekulic, 1983]. In line with this hypothesis, during this study, spontaneous, response, and intergroup encounter calls lasted longer (i.e., males called longer) when at least one resident female called as well than when no females called. An alternative explanation for the prolonged vocal displays when females participated is that both males and females were triggered by the same stimuli that resulted in males to howl for longer and females to join the males. The most obvious stimulus that resulted in prolonged vocal displays, lasting up to one hour [Van Belle et al., 2013a], and increased female participation (72% of howling bouts) was the sighting of neighboring groups. All resident females were more likely to participate and participated for longer during intergroup encounter calls than during spontaneous and response calls. Also adult and subadult males were observed to increase their participation during intergroup encounter calls [Van Belle et al., 2014c]. Such elevated defense efforts by all group members most probably reflect their collective motivation to defend their home range, given that opponents represent a more immediate threat of home range encroachment when they are within sighting distance. The participation by resident females who otherwise only rarely participate might be crucial in mediating the balance of power between competing social groups. For example, during playback experiments that simulated the intrusion of either one or three males, females were most likely to join males during howling bouts when the number of intruders was equal to the number of resident males, indicating that females most likely contributed to group defense when their participation conferred the group with a competitive advantage [Kitchen, 2006]. Assessing female participation in howling bouts during naturally occurring intergroup encounters in relation to numeric superiority between rival groups will shed further light on the role females play during group defense.

In four of the five study groups, one female joined howling males significantly more frequently than the other resident female(s). It is unknown whether these females were more willing to contribute to group defense because they accrued more benefits or incurred less costs as no data are available on long-term reproductive success, physical conditions, weight, or age. However, in the three study groups (Balam, Pakal, and Motiepa) for which systematic data on leadership of collective group movements were collected (only during the first observation period), those females who habitually led collective
group movements [Van Belle et al., 2013b] were those observed to participate in howling bouts most frequently. These results hint at one female attaining a unique social status among resident females that involves regularly participating in collective group defense and habitually leading collective group movements, without otherwise manifesting a dominance hierarchy. A similar association between leadership of group movement and participation in group defense was observed in free-ranging packs of dogs (Canis lupus familiaris [Bonanni et al., 2010a,b]). Bonanni et al. [2010a] hypothesized that group members might be more willing to follow those individuals who are regarded as valuable social partners if their cooperative behaviors are crucial in defeating rival groups. Additional studies will be needed to investigate the association between leadership and cooperative group defense behaviors among females in order to assess this hypothesis in black howler monkeys.

In conclusion, although males are the primary participants in howling bouts, at least one female was observed to join males during over half of these vocal displays. Female calling behavior was not strictly correlated with infant or resource defense, yet all females participated more and for longer during intergroup encounter calls, when they had visual contact with neighboring groups, suggesting that the immediacy of threats by opponents influenced female group defense strategies. In four of the five study groups, one female stood out as the most frequent female participant, suggesting that they play a special role within the group’s social dynamics, not previously recognized for this species. Additional studies on other species of howler monkeys are needed to advance our understanding of how changes in particular social and ecological factors affect female strategies during collective group defense.

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