

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

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ABSTRACT During group defense, the contribution of female black howler monkeys (*Alouatta pigra*) may help deter male intruders; however, their involvement during natural intergroup encounters is facultative. Experimental playback trials simulating potentially infanticidal males were used to examine whether a female's reproductive investment and/or her group's relative fighting ability would influence her participation in loud call displays. Female howlers never responded to recordings without alpha male accompaniment, but their response patterns did not simply mimic his. For example, unlike alpha males, females with small, vulnerable offspring were no more likely than females without infants to participate in howling displays during playback trials. Further, although females without any small infants in their group got closer to speakers than females living in

groups with small infants, males did not respond in the same way. To artificially simulate different "numeric odds" scenarios, recordings of one or three howling males (simulated intruders) were broadcast to females living in groups with 1–3 resident males. Responses were consistent with the hypothesis that females assessed intergroup fighting ability. As in alpha males, the weakest female responses occurred when the numeric odds were against their group. However, whereas alpha males participated most when numeric odds were in their favor, females had the most intense approach responses when the number of defending and intruding males was equal. Females appeared to use a cost-effective strategy, reserving their assistance for when their participation could have the greatest impact. *Am J Phys Anthropol* 131: 73–83, 2006. © 2006 Wiley-Liss, Inc.

Despite substantial size differences in some mammalian species, female members of groups are often active participants in displays or attacks against invading males (reviewed in Cheney, 1987; Smuts, 1987; Packer et al., 1990; Fashing, 2001). For example, in some species, the ability of extragroup males to gain membership in a group is based in part on the behavior directed at them by females (reviewed in Packer and Pusey, 1979; Sekulic and Chivers, 1986; Pusey and Packer, 1987). Females have even thwarted infanticidal attempts of newcomer males in some species (e.g., Collins et al., 1984; Smuts and Smuts, 1993; Pusey and Packer, 1994; Grinnell and McComb, 1996).

Notwithstanding the potential influence of female nonhuman primates in deterring male intruders, their involvement in group defense is facultative in many species (reviewed in Cheney, 1987). Of course, a female should collaborate with companions in group defense if the benefits of her contribution outweigh her personal costs of participating. Such costs and benefits could include the probability of a physical assault being directed at her, the probability of her group winning the encounter, and the probability that a contest loss would have fitness consequences (e.g., based on her reproductive investment and the risk of infanticide). Although a handful of studies quantitatively analyzed the role of female primates during intergroup conflicts (e.g., Cheney, 1981; Cheney and Seyfarth, 1987; Hill, 1994; Perry, 1996; Steenbeek, 1999; Steenbeek et al., 1999; Reichard and Sommer, 1997; Fashing, 2001; Lazaro-Pareo, 2001; Nunn and Deaner, 2004; Sicotte and Macintosh, 2004; Majolo et al., 2005), few used experimental protocols to manipulate

the costs and benefits of female participation (Thomas langurs: Wich et al., 2002a,b, 2004). Here, experimental playback techniques were used to explore the participation of female Belizean black howler monkeys (*Alouatta pigra*) in loud call displays directed at extragroup males.

Black howler monkeys live in groups of 1–3 adult males, 1–6 adult females, and offspring of various sizes (total group size range: 3–15). Relatedness within and among groups is variable due to bisexual dispersal in this species (Brockett et al., 2000a). Groups are not territorial in the traditional sense (i.e., they have a high degree of home-range overlap and do not patrol boun-

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daries; Mitani and Rodman, 1979), but they often act aggressively toward other groups or extragroup males that they see or hear (Horwich and Gebhard, 1983; see Methods). Although the alpha male is the most frequent group member to produce loud calls and/or approach the opposing group (Kitchen, 2004), one or more of the adult females or subordinate males in the group may accompany him. When multiple members participate in an intergroup display, they may do so as a tightly knit, synchronous group, or they may spread out and vary their involvement (Kitchen et al., 2004).

Participation has its costs, particularly when howling displays escalate to approaches and physical battles. During natural intergroup contests, female black howlers have been pursued and thrown from trees by members of other groups (Kitchen, 2000), and females that were captured for marking were often found with scars and wounds (R. James and R. Horwich, unpublished data; see also Crockett and Pope, 1988). However, because infanticide of vulnerable offspring has been documented in this species (Brockett et al., 1999), permitting a "takeover," where a single male or male coalition wrests control of a group of females from another male or group of males, may be even riskier than fighting.

Because they are only rarely observed, few details of female behavior during takeover attempts have been documented in black howler monkeys (Horwich, 1983). However, "takeover" males can transfer from neighboring groups (Horwich et al., 2000), and females (even those with small offspring) have been observed howling, approaching, chasing, and fighting with members of other mixed-sex groups (personal observations; see also Crockett and Sekulic, 1984). An experimental study of the related mantled howler monkey (Whitehead, 1989) suggests that female howler participation may be influential in the outcome of such intergroup contests. Mixed-sex groups that were broadcast recordings containing female vocalizations (female "howl" vocalizations can be easily distinguished from male howls; see Methods) retreated more often than those tested with recordings of males alone (see also Sekulic and Chivers, 1986). Although this suggests that a female's participation is valuable during an intergroup encounter, it is unclear whether this is because she constitutes a threat to interlopers or because her participation indirectly increases the motivation of males resident in her group.

As in other species of howlers (e.g., Sekulic, 1983b; Chiarello, 1995), female black howler monkeys do not always join males in group-level howling displays. During 89 natural encounters between 15 groups, black howler females never vocalized without male accompaniment (Kitchen, 2000, 2004). Although adult females joined males in 46.6% of displays ($n = 61$ of 131 observations made on one or both groups in 89 intergroup encounters), not all females participated equally; only an average of 60.4% of all adult females present vocalized (range: 25–100%).

What factors determine whether a female black howler will assist a male during these displays? The purpose of this paper is to examine the effects of relative group fighting ability and the presence of small, vulnerable offspring on female participation in group defense.

PREDICTIONS

Dependent offspring

Young black howler monkeys are vulnerable to infanticide by newcomer males (Brockett et al., 1999; see Meth-

ods). When facing intruding males, alpha male black howler monkeys are sensitive to the presence of small vulnerable offspring in their group (Kitchen, 2004). Because a female mammal's investment in each offspring is disproportionately large compared to a male's (Trivers, 1972), her aggressive behavior should also be influenced by infanticide risk.

Females with and without dependent offspring were exposed to playback recordings that simulated potentially infanticidal male intruders, to test the hypothesis that an individual's infanticide risk would determine responsiveness. One of two alternative predictions would support rejection of the null hypothesis. First, female black howlers with dependent offspring could respond more aggressively to simulated intruders (by howling and/or approaching) than other female group members (for a possible example, see lions: Spong and Creel, 2004). This strategy might be favored if supporting the alpha male prevents infanticidal attacks. Alternatively, females with infants could be less likely to participate in displays than other females. This strategy might be favored if approaching or calling at intruders is costly to a female. For example, the loud calls of howlers may be energetically costly to produce (reviewed in Kitchen 2004), calling may reduce uncertainties about a female's location, and approaching brings vulnerable offspring closer to potential attackers.

Numeric odds

In theory, larger groups can physically dominate smaller ones; thus, group-level fighting ability based on relative number of participants probably strongly influences intergroup contest outcome (observational evidence reviewed in Cheney, 1987). Experimental evidence has accumulated that at least in lions (females: McComb et al., 1994; Heinsohn and Packer, 1995; males: Grinnell et al., 1995), chimpanzees (Wilson et al., 2001), and male black howler monkeys (Kitchen, 2004), animals attend to the "numeric odds" (i.e., the relative number of challengers in two opposing groups).

To test whether female howler monkeys are also sensitive to the numeric odds, recordings of one or three howling males were played to females living in groups with one, two, or three resident males. When a female's group is outnumbered, the surplus of male intruders could focus their attack on her. Game theory predicts that individuals should avoid battles that they will likely lose (e.g., Maynard Smith and Parker, 1976). Thus, females should avoid participating when the numeric odds are against her group (i.e., when her resident males are outnumbered). An alternative prediction is that a female will participate most when her resident males are outnumbered, because that is when her alpha male is most at risk of being ousted by potentially infanticidal intruders. However, based on size dimorphism in this species (see Discussion), this is an unlikely scenario.

There are two alternative predictions about a female's behavior when facing the same number ("odds even") or fewer males than in her own group ("odds with"). First, females might be most likely to assist when the numeric odds are with her group. In this condition, her group is most likely to win the contest, and her risks of attack by surplus males are lowest. Alternatively, females might be most likely to help when their group and the opposing group contain the same number of males. Game theory suggests that contests should be most intense when com-

petitors are most closely matched and the contest outcome is least predictable (e.g., Maynard Smith and Parker, 1976). In situations where groups are otherwise equally matched in terms of males, female support might be most effective.

METHODS

Study site and population

Black howler monkeys are found in Belize, eastern Guatemala, and southern Mexico (Horwich and Johnson, 1986). A thriving population exists along an approximately 8-km stretch of the Belize River in the Community Baboon [sic] Sanctuary, northwest of Belize City (17°33' North, 88°35' West; Horwich and Lyon, 1990; Silver et al., 1998; Horwich et al., 2001). This area is largely secondary forest with low, broken canopy, making howler monkeys relatively easy to observe. Over 100 monkeys living in the section of the sanctuary surrounding the village of Bermudian Landing have been followed since 1990, and are habituated to human observers (James et al., 1997; Horwich et al., 2001). Subjects for this study were adult females and, with one exception, all females wore ankle bracelets with individualized colored beads. During previous capture, ages were estimated based on tooth wear, and females ranged in age from 6–21 years (mean: 13 years).

Black howler monkeys breed throughout the year, and interbirth intervals average 19.4 months (Brockett et al., 2000b; Horwich et al., 2001). Data on observed infanticidal attacks indicate a reduced interbirth interval of 8–10 months (Brockett et al., 1999). Thus, killing a nursing offspring less than 9 months of age should hasten a female's return to estrus, as demonstrated in red howlers (Crockett and Sekulic, 1984). Female subjects that had offspring vulnerable to infanticide were identified before each trial, using long-term demographic data to determine infant age (James et al., 1997; Horwich et al., 2001).

Natural intergroup encounters

When howlers hear another group, any or all members of a group may respond by sitting quietly (possibly going unnoticed by the other group(s) in the low visibility of the forest), or they may even retreat. However, encounters often result in one or more adults howling and/or approaching the other group. For example, of 85 natural intergroup encounters with behavioural data on both groups, 45% ($n = 38$) resulted in at least one individual escalating the interaction by approaching the opposing group (unpublished data; Kitchen, 2000).

Intergroup interactions in this population are fairly frequent and can occur when another group is seen or heard, up to several hundred kilometers away. For example, observers followed members of randomly chosen groups for one or more morning hours on days when no playback trials were conducted from March 28–June 7, 1997 (unpublished data; Kitchen, 2000). This resulted in 68.5 hr of behavioral data, divided among 34 follows of eight groups. Focal groups produced howling displays during 32.4% of these 34 follows ($n = 11$). Of these 11 howling bouts, 45.5% ($n = 5$) were in response to groups heard howling from 100–200 m away, and 54.5% ($n = 6$) were in response to groups seen or heard less than 100 m away.

Playback stimuli

The hyoid apparatus and larynx are extremely enlarged in males of the *Alouatta* genus, and the air sac that extends into the hollow hyoid likely acts as a resonating chamber (Schön Ybarra, 1988; Fitch and Hauser, 2003). As a result, male howling bouts are extremely loud, prolonged, and low in frequency (see below). During multimale black howler choruses, individual contributions are distinct because voices are offset by a few seconds (i.e., staggered; see also red howlers, Sekulic, 1982b). Because a single male cannot mimic multiple calling males, howling bouts are potentially honest indicators of the minimum number of males in a group (McComb et al., 1994).

Although female howlers also howl, they produce a distinctly different vocalization due to the sexually dimorphic vocal apparatus (Sekulic, 1983b; Whitehead, 1989). Female loud calls were not included in experimental playback stimuli for several reasons. First, this experiment was designed to test a female's response to potentially infanticidal opponents. Howler monkey infanticide often follows a group takeover by a single male or a coalition of males, and females never accompany these males. Second, because females never call without male accompaniment (Kitchen, 2004), it is difficult to isolate their calls for inclusion in recorded stimuli.

Naturally occurring howling bouts can last from 30 sec to over 60 min, and contain loud call periods separated by pauses up to 60 sec in duration (Kitchen, 2000). Loud call periods consist of almost continuous, intense vocalizations for up to 114 sec (mean: 8.7 sec; $n = 290$ loud calls from 15 males). During loud call periods, "roars" are intermittently produced. Roars are the lowest frequency (mean emphasized frequency: 689 Hz; Kitchen, 2000; see also Baldwin and Baldwin, 1976; Drubbel and Gautier, 1993; Whitehead, 1995) and most sustained vocalizations in howler repertoires, and are accompanied by vigorous physical displays (Kitchen, 2000, 2004).

Male howling bouts were recorded from August–September 1994, using a Sennheiser MKH-70 directional microphone (frequency response: 50–20,000 Hz) and a Sony TCD-D7 digital audio tape recorder. All recordings were made directly below and facing the caller. Bouts for stimulus construction were chosen from those elicited by other howling groups 100–200 m away (few good-quality recordings were collected when interacting groups were closer). Takeovers are only rarely observed, and as a consequence it was not feasible to restrict stimuli to this context. However, infanticidal takeovers can be staged by males transferring from neighboring groups (Brockett et al., 1999; Horwich et al., 2000), and there is currently no evidence that calls produced by resident vs. transferring male howlers are different (as seen in Thomas langurs: Wich et al., 2004).

Using Sound Edit 16 bioacoustic software (Walker et al., 1987), approximately 3 min of good-quality loud calling (i.e., containing roar vocalizations and free from background noise) were cut from original howling bouts, and this sequence was repeated once to create five single-male howling bouts (mean duration: 6.12 min). Using Canary waveform analysis software (Charif et al., 1980), there was no significant difference between original and modified versions, based on measurements including bout duration, duration of loud call periods, percentage of bout comprised of loud calling, roaring rate, and mean roar duration (Kitchen, 2000).

TABLE 1. Distribution of 27 females in 12 groups during experimental playback trials that simulated different “numeric odds” (i.e., relative number of male residents to male intruders) with bold cells indicating trials in the which alpha male responded

Group (no. of males) ¹	Offspring present			Offspring absent		
	Odds against	Odds even	Odds with	Odds against	Odds even	Odds with
Bamboo (1)	n/a ²	n/a	n/a	3	3	n/a
Ghost (2)	2	n/a	2 ³	2	n/a	2
Northern A (3)	n/a	2	2	n/a	n/a	n/a
Peninsula (2, 3) ⁴	3	3	3	1	1	1
Vickie (1)	1	1	n/a	n/a	n/a	n/a
Wade (1, 2)	3	n/a	3	3	3	n/a
West Dellas (2, 3) ⁴	1	n/a	1	1	n/a	1
Y Troop (3)	n/a	3	3	n/a	3	3
Baptist (3)	n/a	2	2	n/a	n/a	n/a
Fig Tree (1)	2	2	n/a	n/a	n/a	n/a
Joseph (1)	n/a	n/a	n/a	1	1	n/a
Roxie (1) ⁴	1	1	n/a	1	1	n/a
n _{groups tested} (n _{alpha response}) ⁵	7 (2)	7 (4)	7 (5)	7 (2)	6 (5)	4 (3)

¹ The first eight groups listed, located in northeast study site, were played southwestern call pairs (A₁/A₃, B₁/B₃, and C₁/C₃); the remaining four southwest groups were played northeastern recordings (D₁/D₃ or E₁/E₃). Fifty-five trials were conducted (sample sizes by pair, with decimals indicating three uncompleted pairs: n_A = 5; n_B = 7; n_C = 7.5; n_D = 4.5; n_E = 3.5). Different exemplars were used anytime a group was tested twice in same “odds” condition, and mean response was used for analysis.

² n/a, not applicable.

³ Mean response of all females with or without small offspring in each odds category was used when testing multifemale groups.

⁴ Indicates three groups that contained females with and without offspring concurrently; other groups had to be tested in multiple years to examine both conditions.

⁵ For univariate analyses, each group only contributed one data point for each of two offspring or three odds categories. In other words, data were partitioned separately by presence (n = 10 groups tested) or absence (n = 8 groups) of small offspring, or by numeric odds categories (against, n = 9; even, n = 10; with, n = 7 groups).

However, it is still possible that acoustic differences exist among calling bouts produced by these five different males, and these differences could indicate fighting ability or motivation (e.g., howlers: Kitchen, 2000; D. Kitchen, S. Kenney, and R. Wilson, unpublished data; baboons: Kitchen et al., 2003; Fischer et al., 2004). To reduce the effect of intermale differences, single-male calls (A, B, C, D, and E) were mixed with two-male calls to produce five pairs of recordings in which the same male called alone and in a group of three (i.e., A₁/A₃, B₁/B₃, C₁/C₃, D₁/D₃, and E₁/E₃). Subjects were then played a matching pair, so that the comparison was male A alone vs. in a group of three (A + X + Y), and not male A vs. a threesome such as B + X + Y. Two different two-male bouts were used to create threesomes, further reducing (but not eliminating) the effect of potential quality differences between males (see also below).

A natural multimale howling bout was used as a template in creating three-male stimuli, with staggered onset of individual voices. Each of the 10 howling bouts was a sequence of loud calls (mean loud call duration ± SE = 20.14 ± 8.17 sec), interspersed with pauses (mean pause duration ± SE = 4.34 ± 0.73 sec). When measured under field conditions, amplitudes of recordings did not differ statistically from natural vocalization levels, and there was no effect of number of callers or caller identity on amplitude (measured using a Realistic™ 33-2055 sound level meter, C-weighting, referenced to 20 µP). There was also no statistical difference between single- and three-male calls in several measures, including bout duration, duration of loud call periods, roaring rate, and mean duration of roar (Kitchen, 2000). However, the percentage of the total bout comprised of loud calling naturally increased with additional staggered callers.

Experimental design

All playback trials were conducted during the dry seasons (January–June) of 1995–1997. This study was

done in conjunction with another on the response of males to loud calls. Because black howler monkeys rarely spread out to feed, there is no way to isolate individuals for testing. Thus, to avoid habituation due to repetitive tests of the same group, experiments were designed to test both sexes concurrently. Some field assistants were assigned to male(s) and others to randomly chosen females. Typically, there were enough observers to follow all females in the group (for information on interobserver reliability, see Kitchen, 2000).

Females with or without vulnerable offspring resided in groups with one, two, or three resident males. These six blocks were treated with recordings of one or three howling males (Table 1). The “numeric odds” were calculated as the number of defending males in a focal female’s troop relative to the number of males in the simulated intruding group. This resulted in the following categories relative to the focal female’s group: odds with, odds even, or odds against. This variable combines groups facing similar scenarios. For example, a female living in a one-male group encountering one intruder faces the same numeric odds as a female living in a three-male group interacting with three intruders.

To simulate potentially infanticidal males, only calls of non-neighbors were played to each focal group. Accordingly, groups in the northeast end of the study site (Table 1) were presented only with recordings collected in the southwest end (three possible paired stimuli: A₁/A₃, B₁/B₃, and C₁/C₃), and southwestern groups could hear either of two possible pairs of stimuli recorded in the northeast (D₁/D₃ or E₁/E₃). Because a large pasture (approximately 0.5 km wide, the diameter of 1–2 home ranges) separates the northeastern and southwestern ends of this otherwise continuous site, it is unlikely that groups from the extreme ends see or hear each other regularly. However, calls can sometimes be heard for over a kilometer (Horwich and Gebhard, 1983), depending on habitat, ambient conditions, and the direction a male faces when calling. To further ensure that groups

treated these playback recordings as non-neighbors, broadcasting equipment was set up in what would be a unique direction from which to hear particular males, in other words, anywhere in an area approximately 270° surrounding the focal group. Although subjects may have heard the recorded males in the past, they were not currently neighbors, and thus callers represented a threat to residents (i.e., simulating transferring, potentially infanticidal males).

Because some groups had to be tested in multiple years to ensure that the multiple conditions were met (e.g., females who had offspring in one year but not in the next), an attempt was made to test each group with the maximum number of paired recordings possible (Table 1). However, the mean response to each odds category was used whenever a group was tested with more than one single-male or three-male exemplar. In total, 55 trials were conducted on 27 females in 12 groups (Table 1). To avoid problems with pseudoreplication (Hurlbert, 1984), the mean response of all group females with small offspring and all group females without small offspring in each treatment (i.e., "odds against," "odds even," and "odds with") was used in analyses. Thus, each group of females could only contribute one data point in each of the six possible cells (see footnote in Table 1).

Playback stimuli were broadcast with two Bose 151 environmental speakers raised on 8-m collapsible fiberglass poles and concealed in vegetation fairly close to subjects (mean speaker-subject distance: 45.6 m; range: 28–76 m), along home-range boundaries and near important feeding resources (following Whitehead, 1987, 1989). Speakers were placed 5 m apart when broadcasting three-male recordings, which realistically simulated multiple vocal sources (i.e., males are often spread out during natural displays; see Kitchen, 2004).

The order in which recordings were played to any given group was randomized, and there was no effect of sequence on responses (Kitchen, 2000). All experiments were conducted in the morning, when animals were quietly resting or feeding, and followed a search of the surrounding area to avoid conducting trials when other groups were within 100 m. Trials were aborted (or delayed for at least 1 hr) if focal groups were involved in an intergroup interaction in the 1-hr interval preceding the experiment. To reduce habituation, a minimum 7-day interval (average: 18 days) was maintained between consecutive experiments on the same group, and a 2-day minimum period between experiments with adjacent groups (average: 8 days) or with use of the same recording (average: 18 days). Howlers were exposed to simulated howls at a rate less than 20 times the natural howling rate (Horwich and Gebhard, 1983; Silver et al., 1998; Kitchen, 2004). Monkeys never responded to equipment alone, which for various reasons (e.g., dead batteries) was frequently set up without a trial being conducted.

Data collection

During experimental trials, observers noted all occurrences of vocalizations and/or movements of at least 5 m out of original tree toward the speaker as a categorical measure of a female's willingness to participate in a contest. When females participated, four continuous measures were recorded: 1) duration of howl, 2) latency to howl, 3) latency to begin approaching speakers, and 4) the proportion of the speaker-subject distance covered

during an approach (determined after experiments using a cloth measuring tape and a map of the area trees; Horwich et al., 2001). To determine latency, response start-times were subtracted from the onset of playback recordings. If no reaction occurred within 1 hr after recording completion, latency to respond was recorded as 3,960 sec (i.e., mean duration of recordings plus 1-hr response time). It should be noted, however, that at least one group member responded before completion of the 6-min playback recording in most trials, with the exception of two trials when responses occurred within 2 min of recording completion.

Statistics

Nonparametric analyses (SYSTAT, 1997) were used to examine the effect of five potentially confounding effects on female participation, and to test for separate effects of dependent offspring and numeric odds (both categorical variables) on female participation. An analysis of variance (ANOVA) (Sokal and Rohlf, 1981) was used to examine the relative influence of the independent variables (i.e., dependent offspring presence and numeric odds) on female howl and approach responses. Dummy coding was used for categorical independent variables in the statistical model (SYSTAT, 1997). A backward stepwise process (using the general linear model command in SYSTAT, 1997) selected the best model. Because females never respond without the alpha male in natural interactions among wild howler monkey groups (Kitchen, 2000), a subset of trials in which the alpha male howled and/or approached was also examined separately. This more conservative test further reduced the sample size to 24 adult females in 10 groups (Table 1). Alpha was set at 0.050.

RESULTS

General results

In these experiments, females never responded without alpha male accompaniment. Of the 18 times that the alpha male vocalized, at least one female in his group joined on six occasions (33.3% of trials). Even though females are often active during physical displays, including head throws, lunges, and embracing the alpha male while he continuously calls, female loud calls are often brief and intermittent. Females who howled in these experiments did so for an average of 3 min (i.e., 177 sec; range: 10–633 sec).

Of the 16 times that the alpha male approached the speakers, at least one female from his group joined on 14 occasions (87.5% of trials). Females who approached covered an average of 42.9% of the speaker-subject distance (range: 2–82%). Those who advanced to within view of the speaker paid no apparent attention to the equipment. This was also true for males, who occasionally climbed into the tree with the speaker, but then moved past while vigorously scanning the area, seeming to search for the source of the sound without ever obviously inspecting the speakers.

Because some trials prompted both howling and approaching from both sexes, data were combined to avoid pseudoreplication. In sum, of the 21 total trials where the alpha male vocalized and/or approached speakers, at least one female joined by howling and/or approaching in 16 trials (or 76.2% of all trials). Although the combined results are reported below, results do not

TABLE 2. Spearman correlation (r_s) between five potentially confounding effects and female howler monkey responses to playback trials

	Howl latency		Howl duration		Approach latency		Approach distance	
	r_s	P	r_s	P	r_s	P	r_s	P
Female age	-0.149	>0.05	0.143	>0.05	-0.159	>0.05	0.145	>0.05
Speaker-subject distance	-0.017	>0.05	0.016	>0.05	0.083	>0.05	-0.059	>0.05
Total group size	0.123	>0.05	-0.126	>0.05	0.046	>0.05	-0.020	>0.05
Total adults	0.171	>0.05	-0.157	>0.05	0.213	>0.05	-0.162	>0.05
Total infants	-0.071	>0.05	0.068	>0.05	0.072	>0.05	-0.060	>0.05

TABLE 3. Mean \pm SE female howl and approach responses based on whether or not they had small offspring vulnerable to infanticide (i.e., infant <9 months old)

Response	Offspring present (n = 10)	Offspring absent (n = 8)
Howl latency (sec)	3,591.1 \pm 159.9	3,134.3 \pm 119.6
Howl duration (sec)	41.8 \pm 23.5	4.5 \pm 3.2
Approach latency (sec)	3,219.7 \pm 263.5	3,039.0 \pm 263.7
Approach distance (%)	11.9 \pm 5.4	11.0 \pm 3.0

change if the howling data are analyzed separately from the approaching data.

Potentially confounding effects

Results of a Spearman correlation are presented in Table 2. There was no relationship between female howl or approach responses and five potentially confounding effects (female age, speaker-subject distance, and three group composition measures).

Dependent offspring

In all trials, females without small offspring (n = 8 groups; Table 1) were no more likely to have a shorter latency to call (Mann-Whitney test, $U_1 = 48.0$, $P = 0.397$), a shorter latency to approach (Mann-Whitney test, $U_1 = 34.0$, $P = 0.587$), or to end approaches closer to speakers (Mann-Whitney test, $U_1 = 45.0$, $P = 0.651$) than females with small offspring (n = 10 groups). Although females with small offspring had longer calling bouts than those without small offspring (Table 3), this failed to reach statistical significance (Mann-Whitney test, $U_1 = 32.0$, $P = 0.397$).

Of the subset of 21 trials in which the alpha male howled and/or approached speakers, females with small offspring were no more likely to join by howling and/or approaching (72.7% of 11 trials) than females without small offspring (80.0% of 10 trials; Pearson's $\chi^2 = 0.153$, $df = 1$, $P = 0.696$).

Numeric odds

In all trials, female approach responses were strongly affected by the number of males in their group relative to the intruding group (Kruskal-Wallis test, latency to approach: $H_2 = 7.169$, $P = 0.028$; approach distance: $H_2 = 7.819$, $P = 0.020$; Fig. 1). Whereas females had the longest delays and covered the shortest distances when the odds were against their group (i.e., the number of

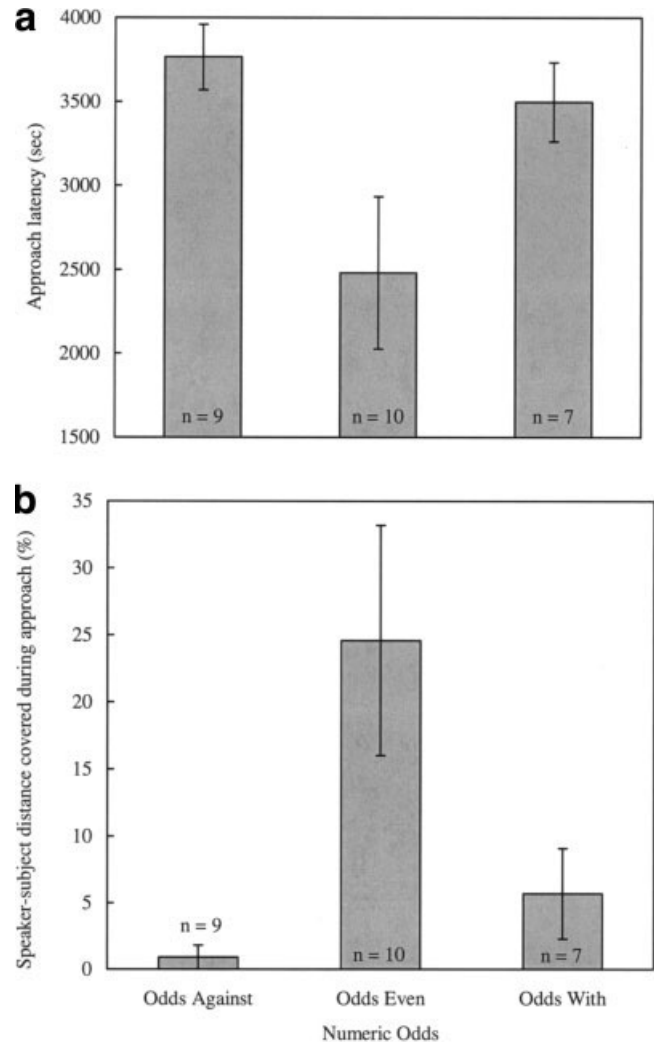


Fig. 1. Mean \pm SE (a) latency to approach and (b) percent of speaker-subject distance covered during approach by female black howler monkeys as a function of numeric odds (i.e., relative number of defending to intruding males). Sample sizes indicate group mean responses (see Table 1 and text for description).

intruding males outnumbered the number of resident males), they were quickest to start traveling and got closest to the speakers when odds were even (i.e., the number of intruding males was equal to the number of resident males).

Even when the alpha male called, females never howled when the number of intruding males outnumbered those resident in her group (Table 4). However,

TABLE 4. Mean \pm SE female vocal response based on numeric odds (i.e., relative number of defending to intruding males)

Response	Odds against defenders (n = 9)	Odds even (n = 10)	Odds with defenders (n = 7)
Howl latency (sec)	3,960.0 \pm 0.0	3,480.0 \pm 247.7	3,629.2 \pm 271.0
Howl duration (sec)	0.0 \pm 0.0	35.9 \pm 22.7	34.2 \pm 33.6

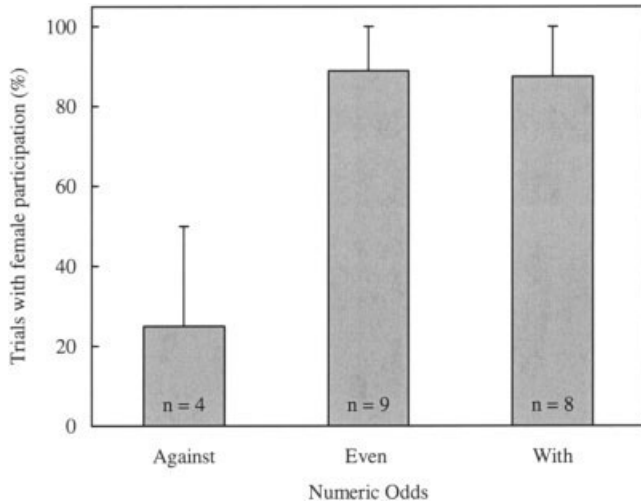


Fig. 2. Percentage of 21 playback trials in which adult female black howler monkeys joined a howling or approaching alpha male, based on numeric odds (i.e., relative number of defending to intruding males).

the effect of numeric odds on female howling responses did not reach statistical significance (Kruskal-Wallis test, latency to howl: $H_2 = 3.111$, $P = 0.211$; howl duration: $H_2 = 3.111$, $P = 0.211$).

Using just the subset of 21 trials in which the alpha male howled and/or approached the speakers, females still responded differently based on the numeric odds. Whereas 88.9% (8 of 9 trials) of females facing “odds even” and 87.5% (7 of 8 trials) of females facing “odds with” their group (i.e., the number of resident males outnumbered the intruding males) joined the alpha by howling and/or approaching, only 25.0% (1 of 4 trials) assisted (by howling and/or approaching) when the number of intruding males outnumbered those resident in her group (Pearson’s $\chi^2 = 7.142$, $df = 2$, $P = 0.028$; Fig. 2).

Relative influence of multiple predictor variables

An analysis of variance was used to examine the relative effects of the presence of small offspring and numeric odds on female responses to all trials. As in the single-factor nonparametric tests, female approach responses were influenced by the numeric odds (Table 5). Results do not fundamentally change if only the subset of 21 trials in which the alpha male responded was used (effect of numeric odds, approach latency: $r^2 = 0.29$, $F_{2,18} = 3.66$, $P = 0.043$; approach distance: $r^2 = 0.34$, $F_{2,18} = 4.70$, $P = 0.023$).

Although males and females both approached speakers during a large number of trials, they did not always travel the same distance (see below). However, to ensure that a tendency to stay close to the alpha male was not driving the female result, this analysis was run again after replacing the average distance that females traveled with the residual of female travel vs. male travel. This was tested using only the 21 trials where alpha males responded, making this a more conservative test. Re-

sponse patterns remained the same (i.e., females traveled the least when the odds were against their group, and the most when the odds were even in terms of relative numbers of males), but now the effect of numeric odds was only marginally significant (ANOVA, $F = 3.70$, $n = 21$, $df = 2$, $P = 0.080$).

There was no effect of the presence of small offspring on female response patterns (Table 5). As a preliminary test of the possible effects of relatives within a group on female responses, “small offspring presence” was substituted with a variable indicating whether or not there were any small infants residing in a group. This analysis was run using only the 21 trials in which alpha males responded. Results remained largely unchanged, with one exception: females without infants in their group tended to get closer to speakers during approaches than females living in groups with infants (ANOVA, $F = 4.35$, $n = 21$, $df = 1$, $P = 0.052$).

Female vs. male responses

Although females never howled or approached speakers without alpha male accompaniment, they did not always join the alpha male during his displays. During 5 of 21 trials in which the alpha male responded, none of the females in the male’s group joined by howling and/or approaching (23.8% of trials); as predicted, three of these trials were when the odds were against the group.

Further, when females did participate, they did not seem to simply mirror the alpha male’s response patterns. For example, when females joined the male during an approach, they did not necessarily stay close to him. Of the 14 trials where both the male and at least one female approached the speakers, only once did they travel approximately the same distance. In 10 of these 14 trials, the females trailed behind the male by 4.0–64.3% of the speaker-subject distance (mean: 26.0%). Surprisingly, in 3 of 14 trials, the females passed the male and ended their approach closer to the speakers by 10.3–33.3% of the speaker-subject distance (mean: 24.4%).

Likewise, the duration of the alpha male’s calling bout was not correlated with the mean duration of female calls (Spearman correlation, $r_s = -0.013$, $n = 21$, $P > 0.100$). Although female contributions to calling bouts might still serve to encourage the alpha male, clearly there are additional sources for his motivation.

Additionally, what best predicted whether an individual would howl and/or approach was different between the sexes. First, although the alpha male howled longer and was quicker to start howling when an infant was present in his group (Kitchen, 2004), adult females did not change their behavior based on the presence of their own offspring. Although the post hoc test reported above indicated that females approached closer to speakers when there were no infants in their group, there was no such effect on alpha male approach patterns (reported in Kitchen, 2004).

Second, the results presented above indicate that females responded slightly differently from the alpha male,

TABLE 5. Results of two analyses of variance testing relative influence of numeric odds and offspring presence on female approach responses¹

Response variable	Predictor variable ²	R ²	df	F	P
Approach latency (sec)	Relative number of males	0.24	2, 35	5.61	0.008
Approach distance (%)	Relative number of males	0.26	2, 35	6.10	0.005

¹ Model selection failed to identify any significant predictors of latency to howl or howl duration.

² Backward stepwise selection identified best models. Presence of offspring had no significant effects.

based on the numeric odds. Although both sexes responded the least when the odds were against their group, the alpha male invested the most in howling and/or approaching when he faced the most favorable odds (i.e., his group outnumbered intruders in term of males; Kitchen 2004). Conversely, females on average had the strongest approach responses when the odds were evenly matched (i.e., the number of simulated intruders equaled the number of adult males resident in her group).

Finally, females did not always act in unison with their female companions. During 9 of 21 trials reported here (42.9% of trials), females within the same group responded differently to playbacks. In 4 of these 9 trials, only one of the females in multifemale groups participated (i.e., in two trials a female approached the speakers, whereas the other female(s) did not; in one trial a female howled, but the other did not; and in one trial a female howled and approached the speakers, but her female companion did nothing). In the other 5 of these 9 trials, all females in multifemale groups participated, but one individual had a stronger response than her companions (i.e., during 4 of these 5 trials one female took much longer than the other(s) to start her approach toward the speakers, and in one trial a female started howling much more quickly and howled longer than her female companion). There were no obvious patterns in these responses in terms of offspring presence, numeric odds, female age, or identity. There was also no apparent intragroup aggression that interfered with female participation (reported in other howler species; Sekulic, 1983b; Crockett, 1984).

DISCUSSION

Dependent offspring

As in other species of howlers (e.g., Clarke et al., 1994; Crockett and Janson, 2000), infanticide has been documented in black howler monkeys, and alpha male black howlers have stronger howling responses to the sounds of simulated intruders when small, vulnerable infants are present in their group (Kitchen, 2004). Given the fitness incentives to deter a takeover attempt, one prediction was that female black howler monkeys with small offspring would also be more apt to join in a group-level display after hearing the howls of strange males. However, given the costs associated with producing loud calls and the increased risk of injury to vulnerable offspring by approaching attackers, an alternative prediction was that females with small offspring would be less likely to join in displays than other females. Contrary to either prediction, females with and without small offspring were equally likely to assist the alpha male by howling and/or approaching the simulated intruders.

Although all trespassing males would be dangerous for a female to contend with, there might be a fitness advantage to discriminating between males attempting a takeover and nontransferring male members of compet-

ing groups. Unlike males transferring between neighboring groups who commit infanticide, the main threat from nontransferring males in a competing group would be loss of a food resource. Therefore, one explanation for the lack of influence of infant presence on females in these experiments is that females do not discriminate between the two categories of male intruders on the basis of vocalizations alone. (Recall that both takeover males and males in competing groups can occur as singletons or as coalitions of two or three males, so the number of males heard in playback recordings should not have affected perception of an infanticidal threat.) Because the encounter rate with takeover males is presumably low (alpha males change tenure every 4 or more years; based on R. Horwich and R. James, unpublished data) compared to the high encounter rate with competing groups (Horwich and Gebhard, 1983), perhaps treating all unidentified intruders as competitors and not as a direct threat to their reproductive investment is the optimal response for females. In Thomas langurs, females were able to distinguish infanticidal strangers from strange males who posed no infanticidal risk based solely on acoustic features of their loud calls (Wich et al., 2003). However, there is currently no indication that the loud calls of resident vs. transferring male howler monkeys differ in the salient ways described for langurs (Bocian et al., 1999; Kitchen, 2000).

The offspring of pregnant females are often killed shortly after birth following takeover events in red howler monkeys (Crockett and Sekulic, 1984). Due to the large energetic cost of gestation, pregnant females might behave in the same way as lactating females (e.g., Sekulic, 1983a). However, observers were unable to distinguish pregnant from cycling females in this study; although black howler monkey females have sexual swellings, there is no evidence of a pattern that would indicate stages in the estrous cycle (D. Kitchen and N. Weber, unpublished data). Thus, it is always possible that the effect of infant presence was imperceptible due to the misclassification of pregnant females in this study.

Finally, the lack of sensitivity to the presence of small offspring might be explained on the basis of intragroup relatedness. In other social mammalian species, the threat of infanticide appears to be a strong selective force that drastically alters female behavior, and may have been an important factor in the evolution of different social systems (reviewed in Smuts and Smuts, 1993). For example, among lions, females are more likely to retreat with their babies (unless their babies are too small to travel) when faced with the sound of an unfamiliar rather than a familiar male (McComb et al., 1993; Grinnell and McComb, 1996). Female lions live in groups with their kin, and defense against male coercion has been postulated as an important factor in the evolution of sociality in this species (Packer et al., 1990).

If a female howler monkey lives in a group with close relatives, she too would derive inclusive fitness benefits by defending her companions' dependent offspring against

strange male intruders, even when she has no small offspring of her own (Hamilton, 1964). In a post hoc test, females living in groups with small infants did not get as close to speakers as those in groups without infants. However, it is not clear if this result reflected inclusive fitness benefits because, unlike lions, variable proportions of both sexes disperse in black howler monkeys (Brockett et al., 2000a). Thus, it is possible that some female howlers resided in groups with relatives, while others did not. Although the census data on this population extend back for 10 years, little is known about relatedness among females in groups.

In sum, despite their greater energetic investment per individual offspring compared to the alpha male (Trivers, 1972), there was no strong evidence that female black howlers changed their aggressive response in relation to their own reproductive investment. Perhaps females have a longer reproductive window, and thus, in terms of lifetime reproductive success, the risk of infanticide may be greater for males. While each offspring is a major portion of an alpha male's lifetime reproductive fitness (in that he probably has limited opportunities for access to groups of females: see Horwich et al., 2000; Kitchen, 2004; red howlers: Pope, 1990; see also lions: Grinnell et al., 1995), a female could mate with the new alpha following a group takeover.

Numeric odds

During simulated intergroup interactions, female howler monkeys attended to the relative number of intruding and defending males (the numeric odds) before joining the alpha male in a display. When the number of males in a female's group matched or outnumbered the simulated intruders, her group had the potential of winning an encounter, and females in these situations were likely (~88% of trials) to assist the alpha male by howling and/or approaching the speakers. On the other hand, when the odds were against their group and thus the risks of an injury and the probability of a losing the contest were highest, females participated the least in contests (25% of trials). A similar overall response was elicited by alpha male howler monkeys: males never howled in response to recordings simulating unfavorable odds unless small, vulnerable offspring were present in their group (Kitchen, 2004). Although females never joined a male by howling when facing unfavorable odds, they once joined the male in approaching intruders when the odds were against them.

Given the risks of attack (males are on average 21% larger than females; Kitchen, 2004; based on unpublished data of R. James, K. Glander, and R. Horwich), it is surprising that females approached male intruders at all, much less when their resident males were outnumbered. Perhaps staying behind and away from the alpha male's protection was even more dangerous than following him. However, sometimes females got closer to simulated intruders than the alpha male, suggesting a willingness to physically contend with, or at least threaten, intruders. Interestingly, subordinate males in multimale groups of howlers did not always assist the alpha male in group defense (Kitchen et al., 2004). Suboptimal levels of "collective benefits," such as group defense, are predicted when associated costs are incurred by only a subset of the group (e.g., by the alpha male in multimale groups of black howler monkeys; Nunn, 2000; Nunn and

Lewis, 2001). The contribution of females to group defense might overcome such collective action problems.

Because a female howler monkey risks severe injury by physically contending with male intruders, her decision to participate in a display may be based on the number of surplus intruders she faces and the impact of her assistance. The most cost-effective strategy for females would be to participate most when their help would have the greatest impact on the outcome of a contest. As predicted, females started approaching with the shortest delays and ended approaches closest to the speakers when the number of males in her group equaled those in the intruding group. This pattern is in contrast to that reported for alpha males, who responded most when numeric odds were most in their group's favor (Kitchen, 2004).

Overall, females appear to be assessing their group's relative fighting ability (in terms of number of males) and reserving their assistance for when the outcome of a contest is least predictable. On the other hand, females appeared to withhold help when it would be most costly to fight (when intruding males outnumbered defending males), or when their group could win without their help (when defending males outnumbered intruding males). Because of the potentially strong impact of female participation on the opposing group's behavior (e.g., Whitehead, 1989) and because subordinate males in multimale groups of howlers do not always assist the alpha male in group defense (Kitchen et al., 2004), a female's optimal strategy based on her own fitness may also be the most beneficial to her companions.

Group-level responses

It is clear that females follow the lead of the alpha male to some degree. Natural intergroup encounters (Kitchen, 2000, 2004) and the experimental results described here indicate that black howler females never howl or approach speakers without alpha male accompaniment. However, patterns among females within and between groups demonstrate that female behavior is not merely a mirror image of the alpha male's behavior. Rather, female participation varies in predictable ways, being greatest when their participation could have the greatest impact. As such, female behavior differs from that of male howlers. Alpha males are most likely to howl when odds are in their favor and when small juveniles are present (Kitchen, 2004). Conversely, subordinate male black howlers were strongly influenced by their own age and the alpha-subordinate relationship, but not by the relative number of challengers (Kitchen et al., 2004). Seemingly complex behavior like group-level defense in black howler monkeys can apparently be predictable to some extent, based on an analysis of each individual's costs and benefits of participation. Although a multimember howling chorus can superficially appear cooperative in this species, the epiphenomenon seems to be largely the outcome of selfish, independent actors (Kitchen and Packer, 1999).

CONCLUSIONS

Experimental playback trials were used to address two factors that might influence female participation during group-level displays at intruding males: numeric odds and offspring presence. When faced with potentially infanticidal males, females did not change their behavior based on whether or not they had a small vulnerable off-

spring. Perhaps female responses are attuned to competing groups, which they encounter at a higher rate than takeover males. Alternatively, pregnant females might respond in the same way as lactating females, but these two groups could not be distinguished in this study. Although there is some evidence that females take fewer risks when any small infant is present in their group, there is no clear evidence that this is based on inclusive fitness benefits because of the variation in intragroup relatedness in this species. Playback trials revealed that females did attend to the numeric odds; a female was least likely to participate when males in the intruding group outnumbered the males in her own group. Further, a female was most likely to participate when her resident males faced an equal number of intruding males. Females appeared to employ a cost-effective strategy of reserving their help for when it would have the greatest impact on contest outcome.

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