



Alpha male black howler monkey responses to loud calls: effect of numeric odds, male companion behaviour and reproductive investment

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When fighting is costly, avoiding contests with superior opponents should confer fitness advantages. Black howler monkeys, *Alouatta pigra*, produce loud calls that reliably indicate the minimum number of male group members. Using playback recordings, I manipulated 'numeric odds' (number of defending to intruding males) to examine whether alpha males use loud calls to assess relative fighting ability, and whether they modify responses to intruders based on relationships with male companions, level of subordinate male cooperation and/or presence of vulnerable offspring in the group. Results indicated that alpha males assess relative fighting ability; howling and approach responses were weakest when subjects faced unfavourable odds. Subordinate male contest participation was inconsistent and alpha males relied less on these unpredictable companions during risky approaches; whereas intruder number affected most howling and approach responses, companion number only influenced howling and orienting duration. Post hoc analyses suggested no effect of alpha–subordinate relationships on alpha reactions. However, preliminary evidence suggested that if subordinates participated, alpha males escalated most when they outnumbered intruders. Alpha males also had shorter howling delays as numeric odds (based on the presence of all subordinates) were increasingly in their favour. Thus, alpha males seemed to escalate in order to signal group-level fighting superiority rather than as a means to gather information on closely matched opponents. Finally, alpha males howled more quickly and for longer at potentially infanticidal intruders if small offspring were present in their group and never called when odds were against their group unless offspring were present, suggesting that contest value was influential.

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As a result of asymmetries in fighting ability, one individual is often superior to another in direct competitive interactions over limited resources (Parker 1974), but all contest participants risk incurring high costs of engaging in these aggressive encounters (e.g. Clutton-Brock et al. 1979). Therefore, according to models developed using evolutionary game theory (e.g. Maynard Smith & Price 1973; Maynard Smith 1974), animals would receive optimal fitness payoffs if they assessed their opponent's ability to control a resource relative to their own and avoided escalating contests they were likely to lose (Parker 1974; Maynard Smith & Parker 1976). Because some vocal or visual signals are too energetically costly for all competitors to produce, they could serve as reliable indicators of an opponent's ability to secure and retain a resource (Zahavi 1975; Krebs & Dawkins 1984). A

growing body of evidence suggests that these assessor strategies are pervasive; for example, in classic studies on roaring red deer, *Cervus elaphus* (Clutton-Brock & Albon 1979; Clutton-Brock et al. 1979) and deep-croaking toads, *Bufo bufo* (Davies & Halliday 1978), individuals avoid persisting in battles with rivals whose vocal signals indicate exceptional prowess.

Although group defence of resources has been proposed as one selective force favouring sociality (e.g. Wrangham 1980; Packer et al. 1990), research on assessment strategies has traditionally focused on pairwise encounters. Assessor models could easily encompass group-level contests if all individuals acted in a collective manner. However, the costs and benefits of participating in a contest are not usually equally distributed among group members and predictions about the epiphenomena of intergroup dominance must therefore be founded on individual advantages (Kitchen & Packer 1999; Nunn 2000; Nunn & Lewis 2001).

Because larger groups can physically dominate smaller groups (e.g. carnivores: Harrington & Mech 1979; Kruuk &

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Macdonald 1985; Packer et al. 1990; primates: Cheney 1987; Isbell 1991; birds: Black & Owen 1989; insects: Adams 1990), animals might first assess the relative size of competing groups before engaging in a contest. If animals assess relative group-level fighting ability, then their response should change based on the 'numeric odds' (i.e. number of defenders relative to number of intruders). Playback studies on the responses of African lions, *Panthera leo* (females: McComb et al. 1994; males: Grinnell et al. 1995) and male chimpanzees, *Pan troglodytes* (Wilson et al. 2001) to manipulated numeric odds provide evidence that members of social units assess relative group fighting ability using loud calls. In both species, group members are highly cooperative during group defence. No test has been conducted on the role of assessment strategies in less cooperative species.

Furthermore, if information on relative fighting ability is gradually accrued during a contest, then the most intense and prolonged struggles should be between animals that are closely matched in fighting ability (Maynard Smith & Parker 1976; Parker & Rubenstein 1981; Enquist & Leimar 1983, 1987). Observational (e.g. Clutton-Brock et al. 1979; Crespi 1986) and experimental (e.g. Clutton-Brock & Albon 1979; Enquist et al. 1990; Leimar et al. 1991) data suggest that contest duration increases and battles intensify as disparities between a pair of combatants decrease. Similarly, members of two competing social groups might prolong a contest when evenly matched, thus gathering information when outcome is least clear. Alternatively, members of a social group might be more likely to sustain a conflict when they outmatch their rivals, signalling their superiority.

Finally, incentives to escalate in an encounter may be based on the value of resources relative to the costs of fighting (Parker 1974; Parker & Rubenstein 1981). In dyadic encounters, individuals seem willing to incur high costs of fighting superior opponents only when the benefits to be gained from disputed resources are extraordinary (e.g. Sigurjónsdóttir & Parker 1981; Austad 1983; Riechert 1984). Similarly, members of social groups might be willing to persist in struggles even when they are outnumbered if the value of winning is especially high, for example, when vulnerable offspring are present in infanticidal species (e.g. McComb et al. 1994). Playback experiments on male African lions supply the best example of the strong effects of resource value relative to fighting costs (Grinnell et al. 1995); despite high potential for injury and death, resident male lions will approach simulated adversaries that apparently outnumber their own group. Due to limited lifetime access to prides of females and low probabilities of gaining a second pride, fitness benefits of maintaining tenure at all costs may provide the incentive for male lion participation in group defence. However, there has been no explicit test of the influence of the presence or absence of vulnerable offspring on an individual's participation in group-level conflicts.

Belizean black howler monkeys, *Alouatta pigra*, live in social groups containing one to three adult or subadult males and one to four adult females (Horwich & Gebhard 1983). After seeing or hearing another group or extragroup

males, any or all members of a group may respond by producing loud calls ('howls') and/or by approaching intruders, or group members may not respond at all (Horwich & Lyon 1990; Kitchen 2000; see also Sekulic 1982a, b; Whitehead 1995). Here, I test predictions that members of black howler monkey groups avoid escalating in encounters when fighting costs outweigh benefits of winning. In natural group-level black howler interactions, one male (the alpha) participates most frequently. Although other adult group members frequently join the alpha male, it is rarely without his accompaniment. In this paper, I focus on the responses of alpha males to playback stimuli. I have discussed the response patterns of subordinate males and females in more detail elsewhere (Kitchen 2000).

Howling is an inherently risky behaviour in that it reduces opponents' uncertainties about the defender's location and fighting ability. In addition, loud (88 dB at 5 m) and prolonged howling bouts (many in excess of 1 h) accompanied by vigorous physical displays are probably energetically costly to produce. This is particularly likely given that a large portion of a howler's diet consists of leaves laden with secondary compounds (Glander 1978; Silver et al. 1998), yet their digestive tracts are not highly specialized and are more similar to those of frugivorous primates (Chivers & Hladik 1980; Milton 1980). Based on the lack of ready energy available from their diets, howlers appear to minimize activity such as travel (Milton 1980).

Nevertheless, a howling display is presumably a less costly alternative to physical fighting. Black howlers in this study population frequently had scars and males and females were often chased, attacked and thrown from trees during battles with other groups (Kitchen 2000). Additionally, the threat of infanticide in this species further increases the cost of direct confrontation (Brockett et al. 1999).

Predictions

Value of small offspring

As with other species of howler monkeys (e.g. mantled howler, *A. palliata*: Clarke et al. 1994; red howler, *A. seniculus*: Crockett & Sekulic 1984), observational and circumstantial data suggest that when immigrant male black howlers enter a group and usurp the resident alpha male they sometimes kill the small offspring of their rivals (Brockett et al. 1999). Black howler monkeys breed throughout the year and interbirth intervals average 19.4 months (Brockett et al. 2000a; 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 oestrus, as demonstrated in red howlers (see Crockett & Sekulic 1984).

Alpha males would increase their lifetime fitness if they protected their vulnerable offspring from potentially infanticidal intruders. Therefore, I tested whether alpha male howler monkeys with offspring vulnerable to infanticide would have stronger aggressive responses to simulated intruders than alpha males without such

offspring. Alternatively, males with small offspring could have weaker responses than those without offspring, implying that remaining quiet and hidden or even fleeing from potentially infanticidal rivals is the optimal strategy.

Relative fighting ability

During multimale black howler choruses, individual voices are distinct because contributions are somewhat 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 (see [McComb et al. 1994](#)). I tested the impact of group-level fighting ability as a function of relative group size by playing recordings of different numbers of non-neighbour males to groups with different numbers of resident males (see [McComb 1992](#)). If an alpha male can evaluate the total number of males in his group relative to the intruding group, he should give the least aggressive response when the opposing groups outnumber his own.

Furthermore, individuals following an assessor strategy could show more than one type of overall response pattern. First, alpha male responses could increase as the relative number of defending males to intruding males (i.e. numeric odds) increases. This would suggest that alpha male howler monkeys are more willing to escalate as 'odds' are more and more in their favour, thus advertising superiority by persisting in energetic displays they were likely to win. Alternatively, response strength could reach a maximum when the number of companions versus intruders is equal. By escalating contests most when they are most evenly matched, alpha males could be using displays as a means of gathering more information about their opponents.

Companion behaviour

Subordinate male black howler monkey participation in group defence is highly facultative (see Methods; [Kitchen 2000](#)). Thus, depending on subordinate cooperation, a three-male group may function as a one- or two-male group. Alpha male black howlers in multimale groups may live with their own grown sons, coalitionary partners or other male residents, including deposed alpha males and their grown sons. There is some evidence that interindividual differences in subordinate contest participation are based in part on the nature of these alpha–subordinate relationships (D. Kitchen, R. Horwich & R. James, unpublished data). Here, I examined whether alpha males modify their responses to intruding males based on their relationship with male companions and/or on the level of cooperation displayed by subordinate males during simulated contests.

METHODS

Study Site and Population

Black howler monkeys are found in Belize, eastern Guatemala and southern Mexico ([Horwich & Johnson 1986](#)). More than 1000 monkeys live along an approxi-

mately 8-km stretch of the Belize River in the Community Baboon Sanctuary, approximately 53 km northwest of Belize City ([Horwich & Lyon 1990](#)). Sanctuary monkeys living near Bermudian Landing Village have been followed since 1990 and I could identify many adults by coloured beads on ankle bracelets ([James et al. 1997](#); [Horwich et al. 2001](#)). In this population, home ranges (approximately 1–6 ha) may overlap by up to 60%. Although an increase in population density since 1985 caused some contracting of home ranges in this area ([Horwich et al. 2001](#)), general home range locations were stable over a period of years surrounding this study (with newly formed groups the exception).

Study Subject

Loud calls by black howler monkeys can occur in a number of contexts: at or before first light; when harassed by people and dogs; while attempting a take-over; or after seeing or hearing a nearby or distant extragroup conspecific. Group members are sometimes very cooperative during vocal battles against other groups. When group members howl in chorus, they often posture and swing around on the same branch, even embracing. At other times, group members call when separated by distances up to 8 m, or they move around during encounters (i.e. moving slowly closer or farther apart, as when one individual charges the other group) and this variability in proximity occurs within the same group. When displays escalate to chasing and physical fighting, many members of both groups are usually involved in the *mêlée*, including adult females and subordinate males.

Still, female and subordinate male participation in group defence is highly facultative. In 131 alpha male howling bouts during natural intergroup encounters (two to three groups per encounter; [Kitchen 2000](#)), 46.6% also contained vocal contributions from at least one adult female. In 112 howling bouts produced by alpha males in multimale groups, 58.9% also contained at least one howling subordinate male. Some subordinates cooperate more consistently than others; for example, in one group a subordinate assisted the alpha in more than 80% of 22 encounters and in another group, a subordinate never assisted the alpha during 13 encounters. There also appears to be a high level of intraindividual variation in participation. For example, a two-male group was observed during 27 intergroup encounters. The alpha male howled at neighbouring groups in 22 of these interactions, with the subordinate joining on 13 occasions (59%).

As in the well-studied red howler monkeys ([Pope 1998](#)), relationships among males in multimale groups seem to vary within and between groups. First, long-term observational data indicate that black howler males may take over groups alone or as members of two- or three-male cooperative coalitions ([Horwich et al. 2000](#)). Preliminary evidence based on marked individuals suggests that at least some multimale coalitions consist of animals from the same natal group ([Horwich et al. 2000](#); R. Horwich & R. James, unpublished data). Because of bisexual dispersal in this species ([Brockett et al. 2000b](#)), females within

a group are not always related and male residents are not permanent. Thus, natal coalitions are not necessarily made up of relatives (see also Pope 1998). Second, intruding male black howlers that successfully take control of females within a group often oust the alpha and other male residents. However, sometimes deposed alpha males and/or their grown sons remain resident in the group (Horwich et al. 2001; R. Horwich & R. James, unpublished data).

Because detailed events surrounding take-overs have only rarely been observed, it is unclear how relative numbers of males, individual fighting ability and/or alpha–subordinate relationships affect contest outcome (Horwich et al. 2000). Results of playback experiments on subordinate members of social groups suggest that although the number of intruders does not influence participation, responses are strongly influenced by the alpha–subordinate relationship (Kitchen 2000; D. Kitchen, R. Horwich & R. James, unpublished data). Subordinate males in short-term associations (always either former alpha males or sons of former alphas) participated in contests much less than did subordinates in long-term associations with alpha males. These latter subordinates were either fully grown males born during the current alpha's tenure, males that were formerly in the same group as the alpha (presumably their natal group) or males that joined the current group with the alpha (seemingly as a coalitionary team).

Based on paternity evidence in a related species (*A. seniculus*, Pope 1990) and observational data on black howlers and related species (Horwich 1983; Crockett & Eisenberg 1987; Brockett et al. 1999), alpha males probably father most offspring born during their tenure. In fact, subordinate black howlers have rarely been observed attempting to mate and only one case of group inheritance by a subordinate, after a dog killed the alpha male, has been observed. Thus, the high level of cooperation by subordinate males in long-term associations is most likely due to inclusive fitness benefits derived by their kinship with the alpha male (Kitchen 2000; D. Kitchen, R. Horwich & R. James, unpublished data).

Modification of Natural Calls

For their small size (adult males average 7 kg and 1136 mm measured from head to tail, $N = 42$; R. Horwich, R. James & K. Glander, unpublished data), howlers produce tremendously loud, low-frequency calls (mean emphasized frequency = 689 Hz; Kitchen 2000; see also Whitehead 1995). The hyoid apparatus and larynx are extremely enlarged in males of this genus and the air sac that extends into the hollow hyoid probably acts as a resonating chamber (Schön 1971; Schön Ybarra 1988; Fitch & Hauser 2003). Naturally occurring howling bouts can last from 30 s to over 60 min and contain loud-call periods separated by pauses up to 60 s (Kitchen 2000). Loud-call periods consist of almost continuous, intense vocalizations for up to 114 s (mean = 8.7 s, $N = 290$ loud calls from 15 males; Kitchen 2000). During loud-call periods, 'roars' are intermittently produced. Roars are the lowest-

frequency and most sustained vocalizations in howler repertoires and are accompanied by distinctive physical postures (Whitehead 1989, 1995; Kitchen 2000).

I recorded male howling bouts during 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. From these recordings, I chose bouts from five single males and two pairs of males as stimuli for playback experiments. I chose only bouts free from background noise, given during daylight hours and elicited in response to distant groups heard howling, the situation I intended to simulate. Because take-overs are only rarely observed, it was not feasible to restrict stimulus to this context.

Using Sound Edit 16 bioacoustic software (Walker et al. 1987), I artificially modified natural bouts to create single- and two-male recordings that were similar in duration (mean = 5.8 min). Using Canary (Charif et al. 1980), I found no significant differences between original bouts and modified versions based on several measurements, including bout duration, duration of loud-call periods, percentage of bout comprised of loud calling, roaring rate and mean roar duration (Kitchen 2000). However, it is likely that individual differences exist and that these differences may indicate an individual male's fighting ability (Kitchen 2000). Thus, to further control for the potential confounding effects of intermale differences, I mixed single-male calls with two-male calls to produce pairs of recordings in which the same male called alone and in a group of three. I used a natural multimale howling bout as a template in creating five experimental pairs, with onset of individual loud-call sequences offset by a few seconds (A_1/A_3 , B_1/B_3 , C_1/C_3 , D_1/D_3 and E_1/E_3). To maximize reactions, I played only calls of non-neighbours/strangers to each focal group. Thus, groups in the northeast end of the study site were presented only with recordings collected in the southwest and vice versa.

When measured under field conditions, amplitudes of recordings did not differ statistically, nor was there an effect of number of callers on amplitude (measured using a Realistic 33-2055 sound level meter, C-weighting, re. 20 μ Pa). There were also no statistical differences between single- and three-male calls in several measures of overall pattern, including bout duration, duration of loud-call periods, roaring rate and mean duration of roars (Kitchen 2000). However, the percentage of total bout duration comprised of loud calling naturally increased with additional staggered callers.

Experimental Design

With the aid of field assistants, I tested 12 alpha males during the dry seasons (January–June) of 1995–1997 (see Kitchen 2000). Because of the subtlety in intragroup interactions among adult howlers, a male was classified as either an alpha or a subordinate before the study based on proximity to females (following Jones 1982; Zucker & Clarke 1986) and on the frequency of involvement in natural group-level interactions. The few subsequent

male–male approach–retreat interactions observed confirmed classifications and no male ranks appeared to change during this study.

Each alpha had zero, one or two male companions and resided in a group with or without small offspring (i.e. still suckling, often riding and less than 9 months of age). I treated each of these six blocks with recordings of one or three howling males (Fig. 1). The numeric odds were calculated as the number of defending males in a focal male's troop relative to the number of males in the simulated intruding group. This resulted in the following categories relative to the focal male's group: odds with, odds even or odds against. This variable combines alpha males facing similar intergroup scenarios. For example, a male living alone encountering one intruder faces the same odds as a male with two companions interacting with three intruders (Fig. 1). I attempted to test each group with the maximum number of paired recordings possible, depending on their location within the study site. This resulted in 60 trials (sample sizes by pair: $N_A = 8$; $N_B = 10$; $N_C = 16$; $N_D = 9$; $N_E = 17$). However, to avoid pseudo-replication (Hurlbert 1984), I used the mean male response in each 'odds' condition. Thus, each male could only contribute one data point in each of the six cells (Table 1).

I randomized the order in which recordings were played to any given group 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 decrease the probability that other groups were nearby. I avoided testing males who had a natural intergroup encounter or howled in the 1-h interval preceding the experiment. To reduce habituation, I maintained a minimum 7-day interval between consecutive experiments on the same group (average = 18 days) and a 2-day minimum period between experiments with adjacent groups or with use of the same recording. Furthermore, howler monkeys were exposed to simulated howls at a rate less than 20 times the natural howling rate (howlers spend 1.5% of their time per month howling, Silver et al. 1998). During two completed experiments, a very distant group was heard howling just before recording completion. I determined possible identities (based on azimuth of the call from the focal group) of these and any other distant groups heard howling in the 1 h following trials and refrained from testing the list of potential nontarget groups for one to several weeks, and then only with a different recording.

Although intruding males can challenge residents from anywhere in the home range, there is some indication that encounters between neighbouring troops occur most frequently near important feeding resources along home range boundaries or in overlap areas (Horwich & Gebhard 1983; Horwich & Lyon 1990; unpublished data; see also Sekulic 1982a; Whitehead 1989). Thus, to maximize responses I attempted to conduct all trials in these areas. Playback stimuli were broadcast with two Bose 151 environmental speakers raised on 8-m collapsible fibre-glass poles and concealed in vegetation (following Whitehead 1987). Speakers were placed 5 m apart when broadcasting three-male recordings, which realistically

simulated many natural cooperative displays. For all recordings, equipment produced maximum amplitudes that were equivalent to natural vocalization levels (Kitchen 2000). Because a large pasture (approximately 0.5 km wide) separates the northeastern and southwestern ends of this otherwise continuous site, it is unlikely that groups on extreme ends see or hear each other regularly. However, calls can be heard for over a kilometre (Horwich & Gebhard 1983) depending on the direction a male faces when calling, habitat and ambient conditions. Thus, to further ensure that males treated these playback recordings as non-neighbours, I attempted to set up broadcasting equipment in directions from focal groups that would be a unique azimuth from which to hear the male(s) on the recording (i.e. anywhere in an area of approximately 270° surrounding the focal group).

Data Collection

During playback trials, we noted all occurrences of vocalizations and movements (of at least 5 m out of original tree towards or away from speaker) by the alpha male. The start and end times of these responses were subtracted from playback recording onset to determine latency and duration of behaviours. Although I defined a howling bout as intense loud calls, including pauses less than 1 min, no test group produced a second howling bout in the hour following playback trials. Approach rate was estimated in meters per second, facilitated by the sanctuary's marked trail system (Horwich et al. 2001). Percentage of speaker–subject distance covered during approaches was approximated after experiments using a cloth measuring tape (mean = 56 m). Finally, we measured male orienting duration, including the initial look towards speakers, subsequent scans of area around speakers and brief glances back and forth from companions to speakers. In all trials where males oriented in the direction of speakers (eyes were not visible in four trials), they did so immediately. Their heads usually snapped up at recording onset and they usually sat up or stood. Several methods were used to eliminate error associated with interobserver reliability in data collection (Kitchen 2000).

If no reaction occurred within 1 h after recording completion, latency to respond was recorded as 3960 s (mean duration of recordings plus 1-h response time). Most responses by alpha males occurred before completion of the 6-min playback recording with the exception of two that occurred within 2 min of recording completion. Males that approached to within view of the speaker paid no apparent attention to the equipment and often continued to move past with clearly vigilant posture, seeming to search for the source of the sound.

Statistics

Nonparametric analyses were used to test the separate effects of small offspring presence and numeric odds on alpha responses. To examine relative influences of each predictor variable, I used an analysis of covariance (Sokal & Rohlf 1981). Included in this model were numeric

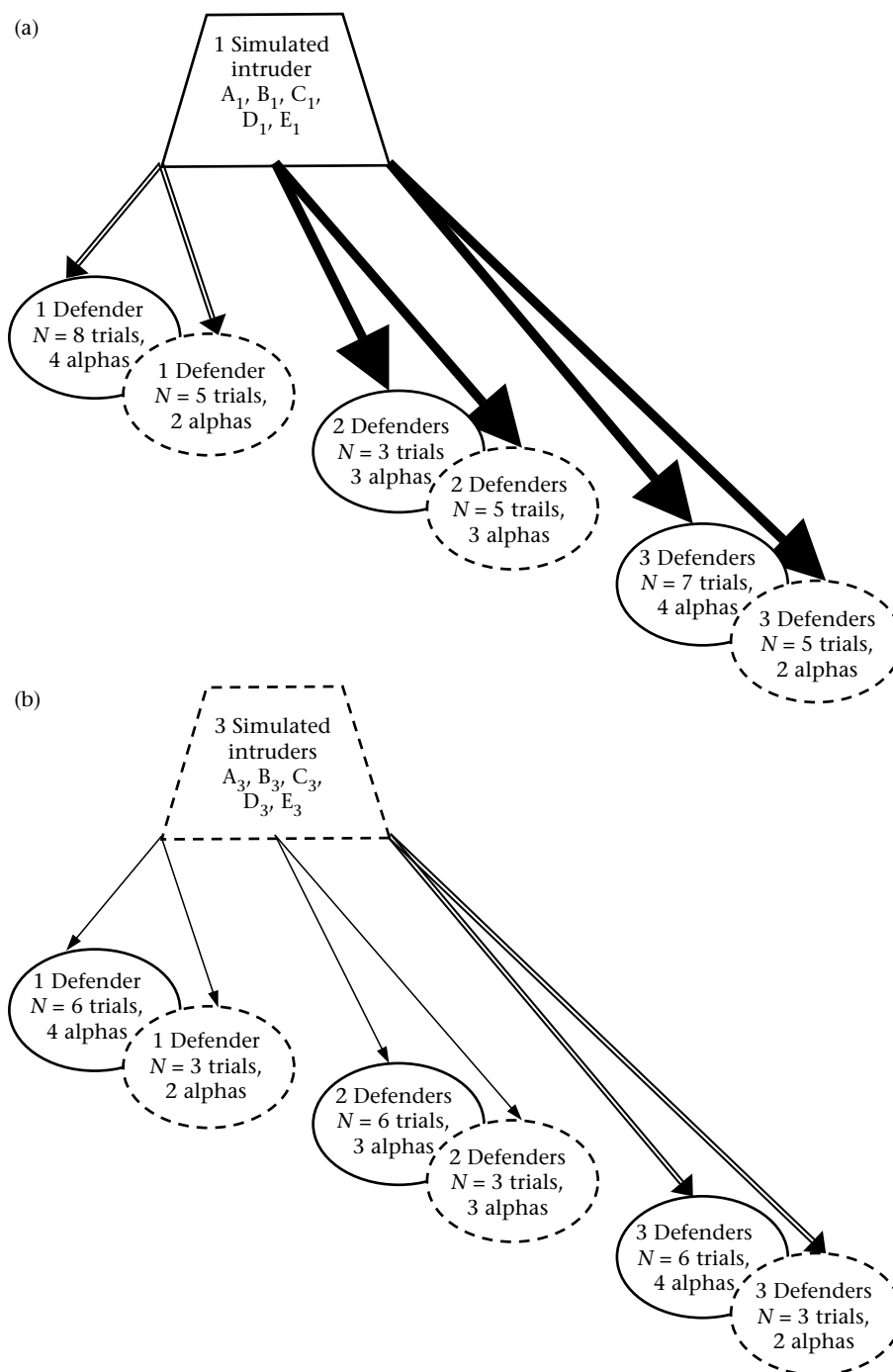


Figure 1. Paired recordings of one or three howling males (e.g. A₁ and A₃) were played to 12 alpha male members of one-, two- or three-male black howler monkey groups, living with (solid ovals) or without (hatched ovals) offspring vulnerable to infanticide. This created tests in which the alpha male's group outnumbered the simulated intruders ('odds with', represented by thick arrows), was outnumbered by the intruders ('odds against', represented by thin arrows) or was equal to the intruders in terms of relative number of males ('odds even', represented by double-lined arrows). A total of 60 trials were completed, but the mean response of each male in each of the six conditions was used for analysis.

odds, presence or absence of small offspring and the interaction term. Additionally, I included two potentially confounding effects as covariates in the model, number of adult females in the group and speaker–subject distance, and included male identity as a random factor. A backward stepwise selection process (using the general

linear model command in SYSTAT 1997) selected the best model. In order to gain a better understanding of the influence of the components of the numeric odds, I repeated this parametric analysis substituting the 'numeric odds' term with 'number of companions' and 'number of simulated intruders'.

Table 1. Alpha males in 12 troops with or without offspring vulnerable to infanticide were subjected to experimental recordings that simulated each 'numeric odds' category (i.e. number of male residents versus number of male intruders)

Troop	Small offspring present			Small offspring absent		
	Odds against	Odds even	Odds with	Odds against	Odds even	Odds with
Bamboo				X	X	
Baptist		X	X			
Fig	X	X				
Ghost	X		X	X		X
Joseph				X	X	
Northern A					X	X
Peninsula	X	X	X			
Roxie	X	X				
Vickie	X	X				
Wade	X	X	X		X	X
West Dellas	X	X		X		X
Y		X	X		X	X
N	7	8	5	4	5	5

The mean response of each male was used for analysis. For parametric analyses, the sample size was the number of males tested in each of the six possible conditions ($N = 34$). For nonparametric analyses, each male only contributed one data point for each of the two offspring (present: $N = 9$; absent: $N = 7$) and three paired numeric odds categories (against versus even: $N = 8$; even versus with: $N = 6$; with versus against: $N = 4$).

Finally, I replaced the numeric odds variable in the model described above with one of two variables, 'functional odds' or 'coalitionary odds', to investigate whether these variables might be better predictors of alpha response than the actual number of subordinates present. It must be stressed that these analyses were post hoc and are used for heuristic purposes only. First, I determined the functional odds categories in the same way as numeric odds (i.e. odds with, even or against), except that I excluded subordinates that did not join the simulated contest by howling and/or approaching speakers. I could then test whether alpha male responses to recordings were influenced by male companion behaviour.

Second, to test for potential effects of alpha–subordinate relationships, I calculated the coalitionary odds by excluding subordinates whose association with alpha males formed under seemingly antagonistic circumstances. Subordinate–alpha pairs were classified into one of two groups during a separate study, which is described in more detail elsewhere (Kitchen 2000; D. Kitchen, R. Horwich & R. James, unpublished data). Five pairs were placed in a 'long-term association' category because the subordinate was either the putative grown son of the alpha or census data indicated that he had a relationship with the alpha that existed for more than 5 years prior to residence in the group, such as that expected with coalitionary partners. Five other alpha–subordinate pairs were classified in a 'short-term association' category because the subordinate was with the alpha for less than 4 years at study onset and was either the former alpha or the grown son of the former alpha. In the current study, the relationship between two alpha–subordinate pairs was unclear and thus they were excluded from this analysis.

Using an example to illustrate the difference between functional and coalitionary odds, consider an alpha male living with two male companions (i.e. a three-male group) hearing a recording of three males. Numeric odds in this

situation would be 'even'. If these two companion males were both the grown sons of the alpha male, coalitionary odds would still be classified as 'even'. However, if neither of these two companions howled or approached during the simulated contest, functional odds would be classified as 'against'.

RESULTS

Single Predictor Analyses

Small offspring

If there were no small offspring present in an alpha male's group, he rarely responded to playbacks and never when the odds were against his group (Table 2). Alpha males with small offspring also howled more quickly (Mann–Whitney U test: $U = 52.50$, $N_1 = 7$, $N_2 = 9$, $P = 0.022$) and for longer ($U = 11.50$, $P = 0.030$) than those males without small offspring (Fig. 2). However, there was no effect of small offspring presence on latency to approach speakers ($U = 36.00$, NS), proportion of speaker–subject distance covered during approaches ($U = 27.00$, NS), rate of approaches ($U = 29.00$, NS) or look duration ($U = 17$, NS). Males rarely retreated and the presence or absence of offspring did not influence this response.

Numeric odds

Alpha males rarely approached speakers when odds were against their group and only when no small offspring were present (Table 3). Although an alpha male's mean latency to howl and approach were longest and mean howling duration, approach rate and approach distance were shortest when odds were against his group compared with when odds were even or with his group (Table 4), only a few of these effects approached statistical significance. There was also no effect of relative numbers on retreats or look duration.

Table 2. Mean percentage of playback experiments that elicited at least one howling response by the alpha male based on the presence or absence of offspring vulnerable to infanticide in their group, partitioned by the numeric odds (i.e. relative number of defending to intruding males)

Numeric odds	Small offspring	N (groups)	Number of trials	% Howl	χ^2_1	P
Against	Present	6	12	66.67	5.24	0.022
	Absent	5	6	0.00		
Even	Present	8	14	62.50	1.50	NS
	Absent	4	8	25.00		
With	Present	6	10	83.33	4.41	0.036
	Absent	5	10	20.00		

Relative Influence of Multiple Predictor Variables

Small offspring

I found no effect of small offspring presence on howling bout duration (Table 5). There was evidence that males howled more quickly when small offspring were present than when they were absent (Table 6), although these results were only marginally significant when companion and intruder number were replaced with the categorical variable 'numeric odds' in the statistical model (Table 5). There was only limited evidence that males tended to orient towards the speaker for longer when small offspring were present than absent (Table 5) and no evidence that small offspring presence influenced alpha male approach patterns.

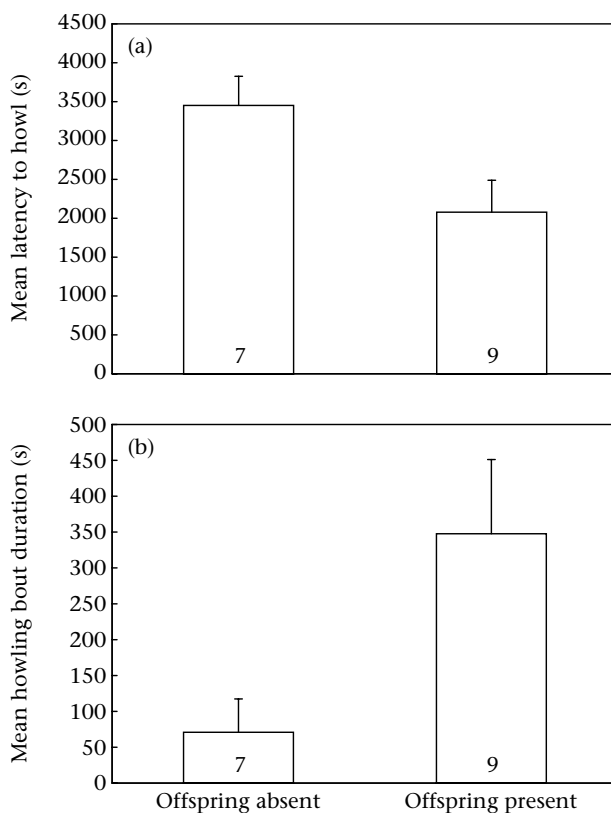


Figure 2. Mean \pm SE (a) latency to howl and (b) duration of howling bouts by alpha male black howler monkeys facing simulated intruders as a function of small offspring presence.

Numeric odds

Numeric odds had an effect on howling duration and a marginal effect on howling latency (Table 5, Fig. 3). Numeric odds also influenced approach latency and distance covered during an approach (Table 5, Fig. 4). Numeric odds did not influence alpha male approach rates or duration of orientation towards the speakers.

Intruder number

The number of intruders affected howling and approach responses (Table 6). Males started howling more quickly, howled for longer, started approaching more quickly and ended approaches closer to speakers when facing one simulated intruder ($N = 18$; adjusted least-squares mean \pm SE: howl latency = 2290.0 ± 247.6 s; howl duration = 329.8 ± 45.2 s; approach latency = 2218.6 ± 267.7 s; approach distance = $26.3 \pm 4.6\%$) rather than three simulated intruders ($N = 18$; adjusted least-squares mean \pm SE: howl latency = 3168.2 ± 247.6 s; howl duration = 181.5 ± 45.2 s; approach latency = 3286.3 ± 267.7 s; approach distance = $12.6 \pm 4.6\%$). Intruder number did not influence alpha male approach rates or duration of orientation towards the speakers.

Companion number

Conversely, the number of companions only affected the duration of an alpha male's orientation and howling responses (Table 6). Alpha males living with two male companions oriented towards speakers and scanned the area for longer periods following playbacks than males living alone or with one companion ($N = 12$; adjusted least-squares mean \pm SE: no companions = 689.2 ± 343.0 s; one companion = 157.1 ± 294.9 s; two companions = 1658.0 ± 385.2 s). Males with two companions also tended to howl for longer periods than males alone or with only one companion (Fig. 5).

Covariate and interaction terms

The interaction between the two components of the numeric odds (intruder*companion number) had a marginal effect on distances covered during approaches (Table 6, Fig. 6); although alpha males living alone tended to end approaches closer to speakers when facing one rather than three intruders, alpha males in multimale troops were less sensitive to changes in intruder number. No other interaction terms had an effect on response

Table 3. Mean percentage of playback experiments that elicited at least one approach response by the alpha male based on the numeric odds (i.e. relative number of defending to intruding males), partitioned by the presence or absence of offspring vulnerable to infanticide

Small offspring	Numeric odds	N (groups)	Number of trials	% Approach	χ^2	P
Present	Against	6	12	0.00	7.04	0.030
	Even	8	14	62.50		
	With	6	10	66.67		
Absent	Against	5	6	20.00	0.93	NS
	Even	4	8	50.00		
	With	5	10	40.00		

variables. Using the model selection process, neither the speaker–subject distance nor the mean number of females present in a group was identified as an influence on any response variables.

Companion Behaviour

Although functional odds had a slightly stronger effect on alpha howling latency than numeric odds, the backward stepwise model selection process failed to identify functional odds as a predictor of approach distance or coalitionary odds as a predictor of either howling latency or duration (Table 7). Thus, although these forms of the relative odds were predictors of some alpha male responses, neither had a stronger overall influence on alpha male responses to simulated intruders than the numeric odds (Table 7).

The overall relationship between coalitionary odds and approach responses was very similar to that produced using numeric odds (e.g. Fig. 4). However, the relationships between functional odds and howling duration,

howling latency and approach latency were all linear (Fig. 7); alpha males had increasingly stronger responses as the functional odds were increasingly in their favour.

DISCUSSION

Value of Small Offspring

As predicted, small offspring presence seemed to influence vocal responses given by alpha males; males howled more often, were quicker to start howling and howled for longer when small offspring resided in their group (Fig. 2). It was particularly striking that when the odds were against them, alpha males only howled if they had small offspring in their group. These data suggest that male howlers might be assessing the value of winning before escalating a contest (Parker & Rubenstein 1981). Investing in energetically costly displays to thwart potentially infanticidal intruders and thereby protect even one small offspring could reap substantial fitness benefits.

Table 4. Mean \pm SE of six alpha male black howler monkey responses to simulated intruders based on the numeric odds (i.e. relative number of defending to intruding males)

Response variable	Odds	\bar{X}	SE	N	H_2^*	P
Look duration (s)	Against	645	123	9	1.58	NS
	Even	1095	236	11		
	With	816	154	7		
Howl latency (s)	Against	2957	460	9	0.43	NS
	Even	2631	449	11		
	With	2419	607	7		
Howl duration (s)	Against	137	81	9	1.51	NS
	Even	326	110	11		
	With	303	139	7		
Approach latency (s)	Against	3657	303	9	6.59	0.037
	Even	2348	491	11		
	With	2425	452	7		
Approach rate (m/s)	Against	0.029	0.029	9	5.79	0.055
	Even	0.041	0.016	11		
	With	0.025	0.008	7		
Approach distance (%)	Against	4.19	4.19	9	6.61	0.037
	Even	31.11	11.78	11		
	With	14.91	3.95	7		

*Kruskal–Wallis test compares mean responses of each male in categories of the numeric odds.

Table 5. Analysis of covariance was used to test the influence of the numeric odds (number of intruding versus resident males) and the presence of offspring vulnerable to infanticide on an alpha male's response, with individual as a random factor and number of adult females and speaker–subject distance as covariates

Response variable	Predictor variable	R^2	df	F	P
Look duration (s)	Small offspring	0.6	1, 21	3.7	0.067
Howl latency (s)	Relative odds	0.8	2, 19	3.4	0.055
	Small offspring		1, 19	4.0	0.059
Howl duration (s)	Relative odds	0.9	2, 20	7.3	0.004
Approach latency (s)	Relative odds	0.7	2, 20	5.6	0.012
Approach distance (%)	Relative odds	0.7	2, 20	4.7	0.021

For each response variable, a backward stepwise selection identified the best model shown above. All response variables also showed significant individual differences. Model selection failed to identify any significant predictors of alpha male approach rate. No covariates or other interactions had significant effects.

However, it remains untested whether these loud calls honestly signal the monkey's willingness to fight.

Because approaching an intruder is such a risky behaviour, it is not altogether surprising that male black howlers with small offspring did not demonstrate an increased likelihood to travel towards opponents. If alpha males had approached simulated intruders without the rest of their group, they would have left their small offspring and females alone and vulnerable. Alternatively, if they had approached the newcomers while accompanied by the rest of their group, they would have greatly jeopardized small offspring by bringing them closer to potentially infanticidal intruders. It is also unlikely that males could protect small offspring during a fight; for example, I rarely observed males carrying offspring (see also Bolin 1981; Horwich & Gebhard 1983) and never during intergroup conflicts. However, males and their small offspring did not flee from aggressors as predicted by the alternative hypothesis. Perhaps stationary howling displays reflect a compromise between flight and fight responses.

Asymmetries in Fighting Ability

Responses to favourable versus unfavourable odds

Overall, these experiments indicated that alpha male black howler monkeys assess the number of males in their group relative to opposing groups during group-level

interactions. As predicted, alpha males did not escalate contests when the outcome of a physical battle was clearly not in their favour; when outnumbered, alpha males were slower to start howling or approaching, howled for shorter periods and ended approaches far from the speakers compared with when odds were even or in their favour (Figs 3, 4). Evidence has accumulated that a wide variety of animals can comprehend ordinal disparities in quantities in a manner similar to counting (e.g. rats: Capaldi & Miller 1988; parrots: Pepperberg 1994; rhesus monkeys: Brannon & Herbert 1998; see also review in Hauser 2000) and a similar cognitive mechanism might explain the ability of black howler monkeys to compare relative group size.

Response patterns

Results were more equivocal when addressing whether alpha male howler responses were strongest when their group was evenly matched in terms of number of males or when they outnumbered the intruders. The latency to howl response seemed to clearly differentiate between these hypotheses; males had shorter delays to begin howling as odds were increasingly in their favour (Fig. 3). However, in other cases (e.g. latency to approach speakers, Fig. 4) results did not differ substantially between the categories 'odds even' and 'odds with'.

Although it is possible that male howlers did not differentiate between the two categories of odds because

Table 6. Analysis of covariance was used to test the influence of number of male intruders, number of male residents and presence of offspring vulnerable to infanticide on an alpha male's response, with individual as a random factor and number of adult females and speaker–subject distance as covariates

Response variable	Predictor variable	R^2	df	F	P
Look duration (s)	Companion number	0.6	2, 22	11.1	0.003
Howl latency (s)	Intruder number	0.7	1, 22	7.3	0.012
	Small offspring		1, 22	7.3	0.012
Howl duration (s)	Intruder number	0.8	1, 21	6.9	0.015
	Companion number		2, 21	3.4	0.051
Approach latency (s)	Intruder number	0.6	1, 23	8.8	0.007
Approach distance (%)	Intruder number	0.7	1, 21	4.8	0.040
	Intruders*companions		2, 21	2.9	0.076

For each response variable, a backward stepwise selection identified the best model, shown above. All response variables also showed significant individual differences. Model selection failed to identify any significant predictors of alpha male approach rate. No covariates or other interactions had significant effects.

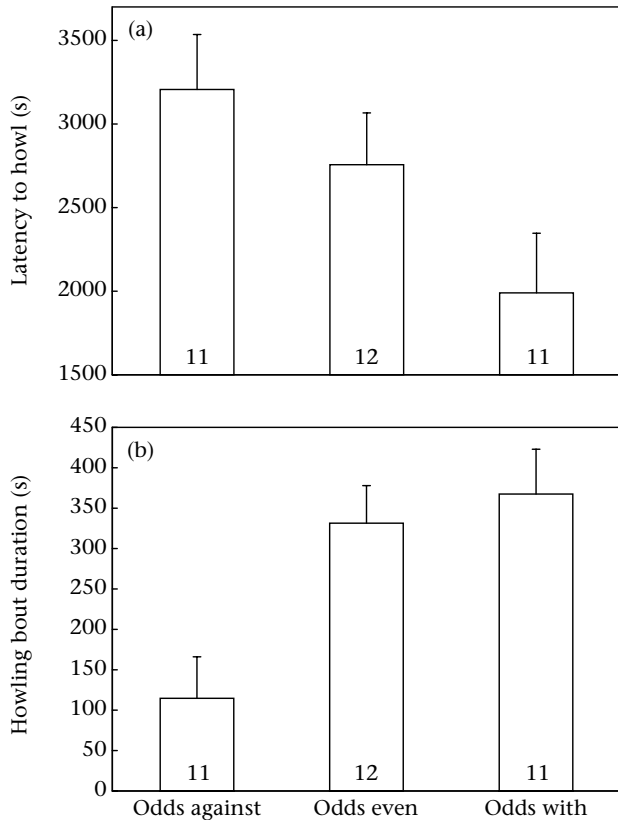


Figure 3. Adjusted least-squares mean \pm SE (a) latency to howl and (b) duration of howling bouts by alpha male black howler monkeys facing simulated intruders as a function of the numeric odds (i.e. relative number of defending to intruding males).

they do not process complex information on group size (Miller 1956), the strikingly weak response by alpha howlers in the 'odds against' trials suggests they do perceive relative differences. It is more likely that the unreliable and varied nature of male coalitions in this species influenced results. Subordinate male black howler monkeys did not consistently join alpha males during natural intergroup displays and when they did assist, their support was not always immediate (Kitchen 2000). Thus, although howling bouts by rival groups honestly indicate the minimum number of males present, they do not necessarily indicate maximum number. Perhaps an alpha male's best response is to escalate equally in both 'odds with' and 'odds even' categories in an attempt to elicit howling from any silent opponents and thereby confirm group size, whereas he would need no additional information when his group was already outnumbered by the current number of callers (see Enquist & Leimar 1983, 1987).

Alpha male members of multiple male groups might also treat 'odds with' and 'odds even' as functionally the same categories because they cannot rely on their own companions to help during intergroup contests. In fact, when looking at the effect of the two numeric odds components, companion number had an effect only on duration of howling and looking responses. Conversely, intruder number had a strong effect on howling and

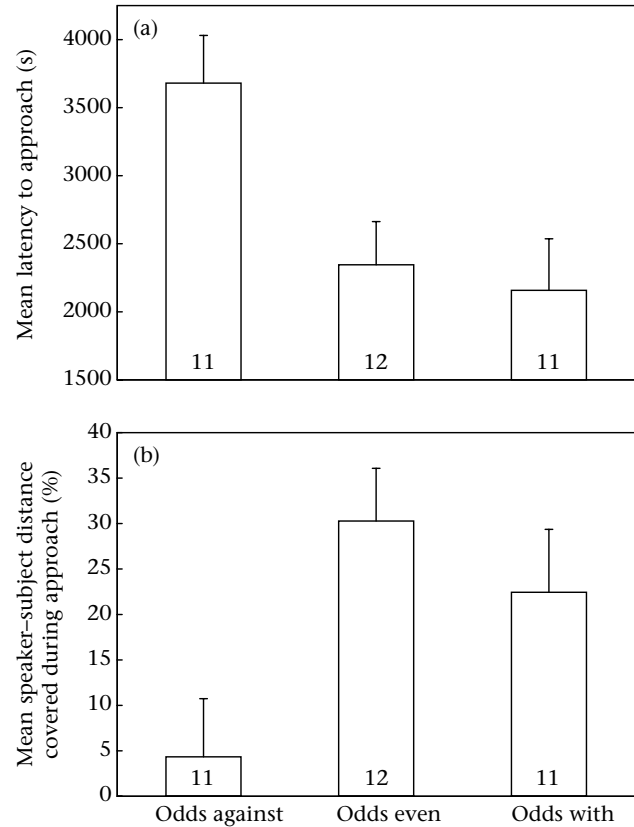


Figure 4. Adjusted least-squares mean \pm SE (a) latency to approach speakers and (b) percentage of the speaker-subject distance covered during approaches by alpha male black howler monkeys facing simulated intruders as a function of the numeric odds (i.e. relative number of defending to intruding males).

approach patterns. Although howling is probably energetically expensive, moving closer to a competitor is probably more dangerous because it increases the probability of physical combat. Unlike more cooperative species such as male chimpanzees (Wilson et al. 2001), an alpha male howler monkey has no guarantee that his companions will assist him during a battle (Kitchen 2000). Even during playback experiments on male and female lions, pride members that approach intruders do so regardless of their companion's apparent cooperation (Grinnell et al. 1995; Heinsohn & Packer 1995). It follows that during very high-risk behaviours, such as approaching rivals, male black howlers would receive more fitness benefits if they did not rely on unpredictable allies.

Responses based on male companion behaviour

To explore the influence of subordinate male cooperation further, I conducted two post hoc analyses. First, because of the varied nature of male associations in this species, some subordinates are apparently more likely to cooperate than others (Kitchen 2000; D. Kitchen, R. Horwich & R. James, unpublished data). Although it would benefit an alpha to be able to predict which potential allies would assist him during a contest, there was little evidence that the coalitionary odds (excluding

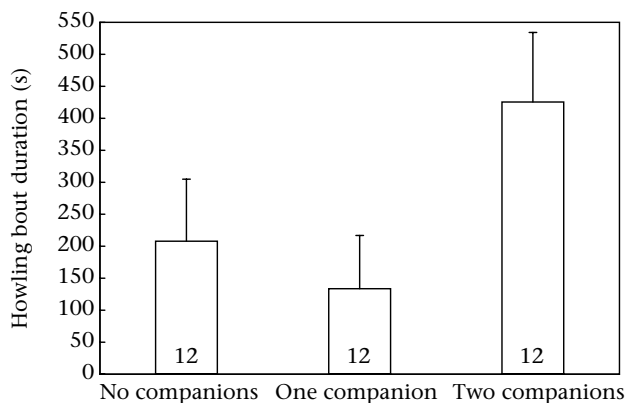


Figure 5. Adjusted least-squares mean \pm SE duration of howling bouts by alpha male black howler monkeys facing simulated intruders as a function of the number of male companions residing in their group.

subordinates in short-term associations) influenced alpha male responses more than the numeric odds. In fact, this predictor variable did not have a significant effect on either measure of howling response.

Alternatively, it would benefit an alpha to alter his behaviour during an intergroup encounter based on the actual cooperation shown by male allies (the functional odds). Although the functional odds had a slightly stronger effect on latency to howl than the numeric odds, this predictor variable had no significant effect on the approach distance response. Thus, although alpha males might modify behaviour based on subordinate cooperation, they were also sensitive to the mere presence of even uncooperative companions. Perhaps in group-level contests that might escalate to physical fighting, the presence of any subordinate males has some sort of dilution effect, incidentally distracting intruders with whom the alpha would otherwise have to contend.

More interestingly, the effect of functional odds on overall response patterns was linear, distinguishing between 'odds even' and 'odds with' categories; males had increasingly stronger responses (longer howling bouts with shorter delays to start howling or approaching) when odds were more and more in their favour. Therefore,

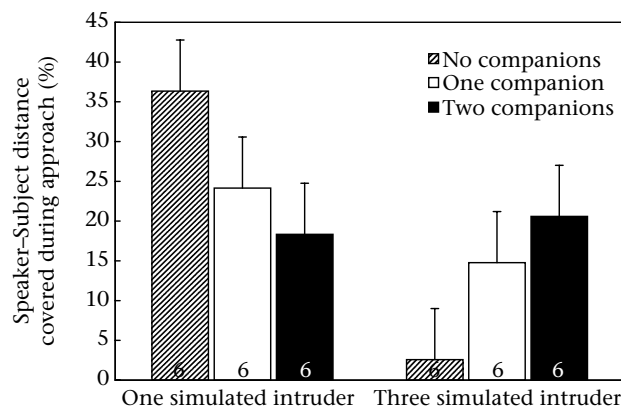


Figure 6. Adjusted least-squares mean \pm SE percentage of the speaker-subject distance covered during approaches by alpha male black howler monkeys as a function of both number of male companions and number of simulated intruders.

response patterns based on both functional and numeric odds seem to best support the hypothesis that alpha males have the strongest aggressive responses when facing the most favourable odds. These results are similar to playback experiments on chimpanzees and lions (McComb et al. 1994; Wilson et al. 2001) and together they suggest that intergroup contests function somewhat differently than dyadic interactions (e.g. Clutton-Brock & Albon 1979; Enquist et al. 1990; Leimar et al. 1991); groups may signal superiority by escalating displays when they are most likely to win, whereas pairwise contestants may escalate to gather more information on opponents when the outcome is least clear.

Response variability among alpha males

Despite the clear influence of relative odds and small offspring on response patterns, alpha males still failed to respond by howling and/or approaching in 58.3% of all 60 trials. It seems unlikely that this is due to habituation (see Methods). Moreover, alpha male black howlers do not always respond to nearby howling neighbours during natural encounters. For example, during one brief study more than 20% of males in 94 natural multiple-group encounters did not reply to a nearby howling neighbour

Table 7. A post hoc comparison of the influence of three categorical variables representing the relative number of defending to simulated intruding males (i.e. odds against, even and with) on howling responses and approach patterns of alpha male black howler monkeys

	Numeric odds				Coalitionary odds				Functional odds			
	R^2	F	df	P	R^2	F	df	P	R^2	F	df	P
Howl latency	0.8	3	2, 19	0.06	0.8	—	—	—	0.8	12	2, 23	0.00
Howl duration	0.9	7	2, 20	0.00	0.9	—	—	—	0.7	6	2, 23	0.01
Approach latency	0.7	6	2, 20	0.01	0.7	5	2, 13	0.03	0.6	5	2, 23	0.02
Approach distance	0.7	5	2, 20	0.02	0.3	4	2, 22	0.03	0.6	—	—	—

The numeric odds were calculated using the actual number of defending males, coalitionary odds were calculated by excluding subordinates whose association with the alpha male formed under seemingly antagonistic circumstances, and functional odds were calculated by excluding subordinates not actively participating (by howling or approaching) in a contest. For each response variable, backward stepwise selection identified the best model, but only the results for the three categories of relative odds are shown above.

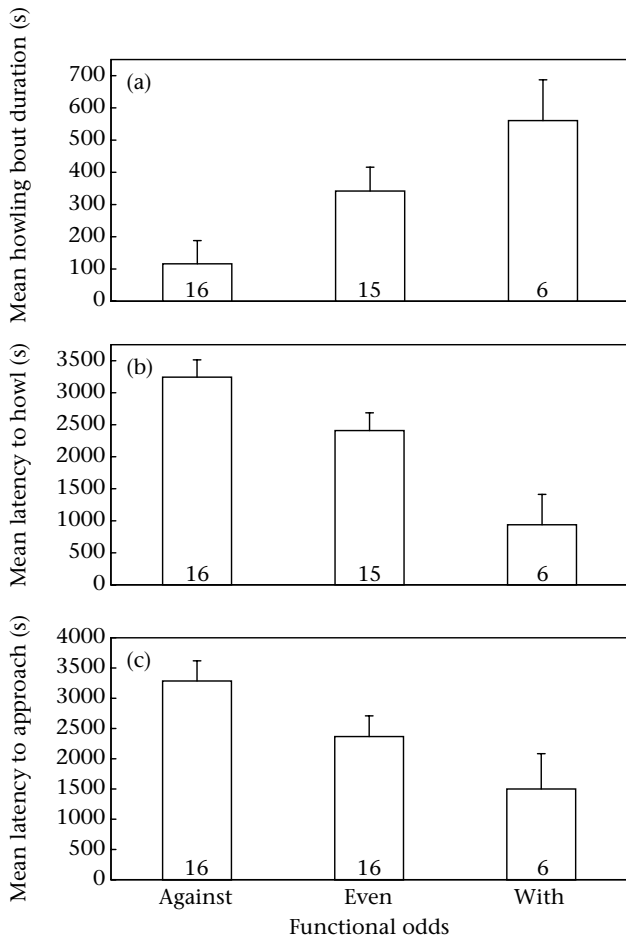


Figure 7. Adjusted least-squares mean \pm SE (a) duration of howling bout, (b) latency to howl and (c) latency to approach speakers by alpha male black howler monkeys based on the functional odds (i.e. number of actively defending males relative to simulated intruding males, calculated by excluding subordinates that did not participate in group-level displays).

(unpublished data) and this number would probably be higher if responses to distant howling groups (the situation simulated in this study) were systematically evaluated.

It is possible that low-level responses are related to energetic constraints. Howler diets are considered a limiting feature of their activity patterns (Milton 1980) and black howlers spend 62% of their day resting (Silver et al. 1998). It may be that remaining quiet and hidden from either take-over males or other groups is an alternative strategy that males adopt when energy reserves are low, as well as when facing superior opponents. It is also possible that male responses changed based on some reliable acoustic feature indicating the fighting ability of individual opponents heard in the recording. Elsewhere I discuss preliminary evidence that some acoustic features of howling bouts are correlated with individual identity, but that these features only appear to influence receiver responses when numeric odds are even, thus when outcome is least clear based on relative odds alone (Kitchen 2000, unpublished data).

Finally, the unreliable assistance of subordinate male companions might once again explain the lack of consistently strong alpha male responses when facing favourable numeric odds (see also *A. seniculus*, Sekulic 1982b). According to collective action models (Nunn 2000; Nunn & Lewis 2001) derived from economic theory (e.g. Olson 1965), alpha male black howlers should invest more in group defence due to the reproductive skew in this species. However, these models suggest that subordinate males are freeloaders if they benefit to some extent by group living and by the exclusion of intruders, yet assist the alpha male infrequently during group-level contests. Suboptimal levels of collective benefits, such as group defence, are predicted when associated costs are incurred by only a subset of the group. Although kinship is thought to overcome such 'collective action problems' (see Heinsohn & Packer 1995 for possible example), this may not be the case in species such as howler monkeys where male–male relatedness can vary within and between groups (Nunn 2000; Nunn & Lewis 2001).

Summary

Although howler monkey group sizes are probably constrained by intragroup feeding competition (see Crockett 1984), the strong effect of the relative numbers of males in the experiments described here suggests that bigger groups are probably better able to defend resources. Even though this implies that members of a unified group would have fitness advantages, groups of black howler monkeys do not act consistently as cooperative units (Kitchen 2000; D. Kitchen, R. Horwich & R. James, unpublished data). During intergroup interactions, alpha male black howler monkey responses are influenced by the presence of vulnerable offspring, the relative number of males in the opposing group and the cooperation of subordinate male companions, suggesting that howlers are assessing the costs of escalating and the value of winning contests before investing in energetic displays.

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