

Intergroup encounters in Honduran mantled howler monkeys (*Alouatta palliata*)

A thesis presented by

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Introduction

Among social animals, we often see costly behavior from one individual that benefits the entire group. Why is one individual willing to risk injury for the good of the group? Collective action framework suggests that these individuals may benefit asymmetrically as compared to other group members because they have the most to gain by exhibiting such costly behaviors (Nunn 2000). One of the best situations to examine collective action framework is an intergroup encounter, that is, situations where members of one group interacts with members of another group (or solitary individuals), usually in antagonistic situations (Kitchen and Beehner 2007). Intergroup encounters are common occurrences across primate taxa, as resource-rich territories and females often represent valuable resources that groups wish to defend (e.g., Verreaux's sifaka, *Propithecus verreauxi*, Jolly 1966; white-faced capuchins, *Cebus capucinus*, Perry 1996; red colobus monkeys, *Piliocolobus* spp., Struhsaker 1975; vervet monkeys, *Chlorocebus pygerythrus*, Cheney 1981; mountain gorillas, *Gorilla gorilla beringi*, Sicotte 1993). Previous evidence suggests that *who* participates (i.e., males, females, or both males and females) indicates which individuals stand the most to gain from keeping other animals out of their group.

One hypothesis for who participates in intergroup encounters is that males will invest more than females in costly behaviors to defend the group. This hypothesis stems from the differential investment of each sex in reproductive events. Because females invest a greater amount of time and resources into reproduction than males do (Hamilton 1974), this creates a conflict of interest where, because males are limited by number of matings and females by food (Trivers 1972), males should mate with as many females as possible, but females should invest heavily in each offspring. Thus, males should participate in intergroup encounters to defend mates (and, where infanticide is a prevalent selective force, infants as well), while females should participate to defend infants and food resources necessary to support this costly investment (Kitchen and Beehner 2007). If males are defending mates, then they should participate in intergroup encounters more often when the female-male sex ratio is high. Females should participate when they have an existing investment in the form of a dependent infant.

Some intergroup encounters result in serious injury or death, including infanticide. Infanticide as a reproductive strategy can be defined as an extra-group male (or males) entering a group and killing the infants present. Females whose infants are killed stop lactating and become reproductively available more quickly as compared to females whose infants are not killed, and males who participate in infanticide gain more mating opportunities than males who do not (Hrdy 1977). In primate species affected by infanticide, males should participate in intergroup encounters more often when the infant-male ratio is high (i.e., when the number of infants in a group is high relative to the number of adult males).

Intergroup encounters among howler monkeys (*Alouatta* spp.) primarily take the form of howling bouts. Loud calls (i.e., "howls") are species-specific high amplitude vocalizations made possible by enlarged hyoid bones in the neck (Hershkovitz 1949). Loud calling is thought to be a male strategy used to determine the size and competitive ability of other males (Sekulic and Chivers 1986, Preuschoft and van Schaik 2000), while incurring very few costs for the males involved. This is important because *Alouatta* species typically have a diet of high-fiber content leaves, which leaves little energy to

devote to physical encounters (Milton 1980). This type of behavior, as opposed to the highly physical competition exhibited by some primates (e.g., baboons, *Papio* spp. Barton *et al.* 1996), is consistent with signaling theory. Signaling theory proposes that, because fighting is costly for both “winners” and “losers”, individuals should signal their strength prior to engaging in costly physical contests. *Alouatta* loud calls, like all signals, are traits that have evolved to reduce the uncertainty that comes when to individuals (that do not “know” each other) must rapidly make a decision to fight or mate (Seyfarth *et al.* 2010). Conflicts should only escalate to aggression if both individuals are closely matched in fighting ability (Maynard-Smith and Packer 1976), particularly when benefits outweigh costs for the males involved (Kitchen 2004).

Alouatta are a good model for addressing the question of resource defense because different species behave differently during intergroup encounters. In some *Alouatta* species, only males howl during intergroup encounters, possibly to gain intergroup dominance and/or mating opportunities (Kitchen and Beehner 2007). Female *Alouatta palliata mexicana* (Mexican howler monkeys), for instance, do not produce true loud calls (Ryan *et al.* 2008). The fact that the females do not participate suggests that females may actually “want” other males to invade the group to become potential mates. In other species, both males and females howl, suggesting that females may also have a stake in keeping males out – possibly to avoid infanticide by these incoming males. For example, black howler monkey (*Alouatta pigra*) females howl in response to potentially infanticidal male intruders (Kitchen 1996).

Loud calls in these species are important because they serve to prevent potential group takeovers by extra-group males. Males that invade successfully become dominant and receive priority of access to resident females. Because extra-group males are reproductively threatening to males (in the form of mate acquisition) and females (in the form of infanticide), both sexes should participate in intergroup encounters at higher rates when loud calls originate outside of their groups (intergroup calls) as compared to within their groups (intragroup calls).

Honduran mantled howler monkeys (*Alouatta palliata palliata*, hereafter referred to as *A. palliata*) are large New World monkeys distributed through Mexico and Central and South America (Jones 1980). Groups are multi-male, multi-female (Chapman and Balcomb 1998) and are composed of eight to 23 individuals on average (Crockett and Eisenberg 1987). *A. palliata* are polygynous with high-ranking males dominating mating opportunities (Carpenter 1934), and there is evidence that infanticide can be an effective male reproductive strategy (Clarke 1983). *A. palliata* is one of the few primate species that can live in forest fragments, and those that live at high population densities have adaptable home ranges, diets, and activity patterns (Cristobal-Azkarate and Arroyo-Rodriguez 2007). Both male and female *A. palliata* juveniles disperse from their natal groups (Glander 1992).

A. palliata groups at Rancho Manacal, Honduras have been monitored with respect to behavior, diet and activity, and vocalization since 2009. The following information about Rancho Manacal was received from Dr. Kathy Slater, Operation Wallacea. The population lives at high population densities in fragmented forest patches and feeds on leaves, but also fruits and flowers. This suggests that females at Rancho Manacal are not as limited by diet as those in other *Alouatta* populations. Females in this population only very rarely produce loud calls (only two cases were documented over

four years). This is typical across *A. palliata* populations (Sekulic and Chivers 1986). Females do, however, exhibit vigilance when they or their infants are threatened. Because vigilance is the only observable measure of “interest” in a howling bout, I will use it as a proxy for “participation” in intergroup encounters throughout this study. The males at Rancho Manacal are known to call not only in the context of intergroup encounters, but also in response to other loud noises, including trucks, thunder, heavy rain, people, and sounds from the neighboring water purification plant.

Groups at Rancho Manacal are arranged linearly such that each group is flanked by one or two neighboring groups (Fig. 1). Although several neighboring groups have overlapping home ranges, individuals from non-neighboring groups are unable to enter each others’ territories. When neighboring groups come into close physical proximity to one another, howling bouts typically ensue, but takeovers are rare, and (although observed in this species more generally), infanticide has yet to be documented at this particular site. Because groups at Rancho Manacal can only be invaded by neighboring groups, both males and females are expected to participate in intergroup encounters at higher rates when calls originate from neighboring groups as compared to non-neighboring groups.

That both male and female *A. palliata* appear to participate in intergroup encounters at Rancho Manacal suggests that the outcome of howling bouts is an important selective force in the lives of all group members in this study population. Therefore, the frequencies of male loud-calling and female vigilance during intergroup encounters can tell us about the “interests” of the group members with respect to fitness. Animals should participate at higher rates when they have more to lose. In summary, I make the following hypotheses and predictions:

Hypothesis 1: Both male and female *A. palliata* at Rancho Manacal “participate” in intergroup encounters.

Prediction 1a: Males will be more likely to respond vocally to intergroup calls than to intragroup calls or other loud noises.

Prediction 1b: Females will be more likely to exhibit vigilance in response to intergroup calls than to intragroup calls or other loud noises.

Hypothesis 2: Intergroup encounter participation will be affected by the presence of defensible resources.

Prediction 2a: Male call rate will increase as the female-male ratio increases.

Prediction 2b: Male call rate will increase as the infant-male ratio increases.

Prediction 2c: Females with infants will be more likely to exhibit vigilance in response to male loud calls than females without infants.

Hypothesis 3: Intergroup encounter participation will be affected by call origin.

Prediction 3a: Males will be more likely to respond vocally to intergroup calls that originate from neighboring groups than to non-neighboring groups.

Prediction 3b: Females with infants will be more likely to exhibit vigilance in response to intergroup calls that originate from neighboring groups than to non-neighboring groups.

Hypothesis 4: Intergroup encounter participation will be affected by numeric odds (i.e., the number of males in the focal group relative to the number of males in the “competing” group will predict whether animals participate).

Prediction 4a: Males will be more likely to respond vocally to intergroup neighboring calls when the neighboring group has fewer males than the focal group (i.e., “odds for”), than when the neighboring group has more males than the focal group (“odds against”).

Prediction 4b: Females with infants will be more likely to exhibit vigilance in response to calls originating from neighboring groups when numeric odds are “for” rather than “against” their focal group.

I will discuss how loud calling affects *A. palliata* intergroup and intragroup behavior at Rancho Manacal, particularly who participates in intergroup encounters, and in what contexts.

Methods

Study site and subjects

Fieldwork was conducted at Rancho Manacal, a privately owned sugar cane plantation with adjacent forest fragments and cattle ranch, in Northwestern Honduras. I collected data from June to August 2012. Supplemental data from 2009-2011 was obtained with permission from Dr. Kathy Slater. Observations were collected on two groups each day, alternating between morning (5:00 AM to 12:00 PM) and afternoon (12:00 PM to 6:00 PM) sessions. Number of morning and afternoon observations and total time watched, were evenly distributed for all groups.

A. palliata study subjects were habituated to the presence of human observers. Eight groups were located in and directly adjacent to Rancho Manacal (Fig. 1). Although individuals were not known, we always know how many and the demographic categories (i.e., adult males, adult females, infants, and juveniles) of all individuals in the groups. Group size ranged from 14-45 individuals (Table 1) and were composed of adult males, adult females, infants, and juveniles. Adult males were visibly larger than females and had conspicuous “beards”. Adult females were larger than juveniles and had lighter colored mantles than all other age-sex classes (see Carpenter 1934 for complete age-sex descriptions). Adult females with infants were defined as those with infants on their backs or in close proximity for a majority of the focal. Because we had no kinship data, we assumed that these were the infants’ mothers for the entire focal.

Behavioral data

Instantaneous scan samples at 10-minute intervals (Altmann 1974) were used to obtain background behavioral data and total time watched for each group annually. Male loud calls were recorded *ad libitum*, noting which group made the call (to be later coded as intragroup or intergroup and for intergroup, either neighboring or non-neighboring) and the number of male callers. Loud calls in this study were defined as any long-distance, inter-group acoustic signals produced by males (i.e., type 1 loud calls; Gautier and Gautier 1977). Intragroup calls were produced from males within the focal group and intergroup calls were produced by males outside of the focal group. Neighboring group calls were produced by males in groups directly adjacent to the focal group, while non-

neighboring group call were produced by males in groups not directly adjacent to the focal group. I also recorded female response, or the behavior (vigilant or not vigilant) immediately following male loud calls for all adult females with and without infants in the focal group. Vigilance was defined as an individual actively looking in the direction of an external stimulus (generally a loud call or another loud noise) for any duration of time. As with calling behavior for males, vigilance in response to male calls was an all-or-none response.

Data analysis

I used chi-square analyses to determine whether observed probabilities of loud call response in males and vigilance in females were significantly different from expected during risky situations. Specifically, male loud calls were categorized as either a "response" or "no response" to another call. Males were recorded as "responding" if they called in response to any other call (intragroup or intergroup) within 5 minutes. Calls were also categorized as intergroup (if the call was made in response to a male outside of the focal group or within 15 minutes of a howling bout between two or more groups), intragroup (if the call was made in response to a male inside of the focal group and no intergroup calls had been made in the past 15 minutes), or "other" (if the recorded call or the initial call of an intragroup bout was made in response to another loud noise, usually vehicles, people, or machinery at the water purification plant). Group call rates were then calculated for each group per year based on total observation time. Female behavior immediately following any loud calls (intragroup or intergroup) was recorded as either "vigilant" or "not vigilant". Similarly, group vigilance rates were then calculated based on total observational time. Chi-square analyses were then conducted. In what follows, I elaborate on how I calculated expected distributions for chi-square analyses.

Prediction 1a: Males will be more likely to respond to intergroup than intragroup calls. First, I calculated expected proportions based on the proportion of intergroup, intragroup, and other calls to all calls observed. I then multiplied these proportions by the number of male responses and non-responses observed.

Prediction 1b: Females with infants will be more likely to exhibit vigilance in response to intergroup than intragroup calls. First, I calculated expected proportions based on the proportion of intergroup, intragroup, and other calls to all calls observed. I then multiplied these proportions by the number of vigilant and non-vigilant responses observed for all adult females.

Next, I tested for a normal distribution for loud call rate, sex ratio (number of adult females/number of adult males in the focal group), and infant-male ratio (number of infants/number of adult males in the focal group). All variables were normally distributed (Kolmogorov-Smirnov test: $p > 0.05$). Loud call rate was defined as the total number of loud calls produced by all males per year of observations based on total observation time. Therefore, each group is represented 4 times in the analysis (one rate for each year). Although each group is not necessarily an independent data point, I feel justified including each point because all groups are equally represented. For predictions 2a and 2b, I used linear regression analysis to test whether the annual male loud call rate

increased with sex ratio and infant-male ratio, respectively. All remaining predictions were tested using chi-square analyses.

Prediction 2c: *Females with infants will be more likely to exhibit vigilance in response to male loud calls than females without infants.* First, I calculated expected proportions based on the proportion of adult females with and without infants to all female observations. I then multiplied these proportions by the number of vigilant and non-vigilant responses observed for all females.

Prediction 3a: *Males will be more likely to respond to neighboring than non-neighboring group calls.* First, I calculated expected proportions based on the proportion of neighboring and non-neighboring calls to all calls observed. I then multiplied these proportions by the number of male responses and non-responses observed.

Prediction 3b: *Females with infants will be more likely to exhibit vigilance in response to neighboring than non-neighboring group calls.* First, I calculated expected proportions based on the proportion of neighboring group and non-neighboring calls to all calls observed. I then multiplied these proportions by the number of vigilant and non-vigilant responses observed for females with infants in response to intergroup calls.

The next few predictions involve “numeric odds”. Numeric odds (i.e., number of males in the focal group versus number of males in the caller group) are used to simulate the number of defending to intruding males (Kitchen 2004). Odds can either be “for”, “against”, or “even”. “Odds for” means the focal group has more adult males than the neighboring group and “odds against” means the focal group has fewer. “Odds even” suggests both groups have the same number of adult males. Note that no neighboring groups in this study were “odds even”. I used the number of males rather than the number of callers because, given the high density at Rancho Manacal, animals presumably know the number of males in their neighboring groups even if only some of the males are participating in a given howling bout.

Prediction 4a: *Males will be more likely to respond vocally to intergroup neighboring calls when numeric odds are for, rather than against, their focal group.* First, I calculated expected proportions based on the proportion of neighboring group calls produced when odds were for and odds against the focal group. I then multiplied these proportions by the number of male responses and non-responses observed.

Prediction 4b: *Females with infants will be more likely to exhibit vigilance in response to calls originating from neighboring groups when numeric odds are for, rather than against, their focal group.* First, I calculated expected proportions based on the proportion of neighboring group calls produced when odds were for and odds against the focal group. I then multiplied these proportions by the number of vigilant and non-vigilant responses observed for females with infants in response to neighboring group calls.

Treatment of outlier groups: Upon visual inspection of the data, it became clear that data from Group 7 consistently skewed my results. Group 7 is unusual for several reasons. First, they only has one neighboring group (as does Group 6). Second, their home range is physically separated from all others and therefore this group may feel less threatened by the calls from other groups in general (Fig. 1). Finally, Group 7 probably hear fewer, less clear vocalizations as compared to all other groups. For these reasons, I felt justified removing Group 7 from all future analyses.

I used SPSS and Excel for all statistics and statistical significance was set at $p < 0.05$.

Results

Predictions 1a-b. Observed male response rates to intergroup, intragroup, and other calls were significantly different than expected based on chance (Chi-square test: $\chi^2 = 242.87$; $p < 0.001$; Fig. 2). Males responded more frequently than expected to intergroup calls and less frequently to intragroup and other calls than expected, with a higher response rate to intergroup calls. Additionally, observed female vigilance rates to intergroup, intragroup, and other calls were significantly different than expected based on chance (Chi-square test: $\chi^2 = 82.22$; $p < 0.001$; Fig. 3). Females responded *more frequently* than expected to intergroup calls and *less frequently* than expected to intragroup and other calls than expected, with a higher vigilance rate for intragroup than other calls.

Prediction 2a. Male loud call rate was significantly related to sex ratio, with higher rates associated with higher sex ratio (i.e., more adult females per male; Linear regression: $R = 0.48$; $p = 0.01$; Fig. 4).

Prediction 2b. Male loud call rate was not significantly correlated with infant-male ratio ($R < 0.05$, $p = 0.83$; Fig. 5).

Prediction 2c. For all male calls, observed vigilance rates in adult females with and without infants were significantly different than expected based on chance (Chi-square test: $\chi^2 = 294.00$; $p < 0.001$; Fig. 6). Adult females with infants exhibited vigilance more frequently and adult females without infants exhibited vigilance less frequently than expected.

Predictions 3a-b. Male response rates to intergroup calls originating from neighboring groups and non-neighboring groups were significantly different than expected based on chance (Chi-square test: $\chi^2 = 21.37$; $p < 0.001$; Fig. 7). Males responded more frequently than expected to both neighboring and non-neighboring calls, with higher response rates for neighboring than non-neighboring calls. The observed vigilance rates for adult females with infants to calls that originated from neighboring groups and non-neighboring groups were significantly different than expected based on chance (Chi-square test: $\chi^2 = 55.20$; $p < 0.001$; Fig. 8), with neighboring group calls eliciting vigilance more frequently and non-neighboring group calls eliciting vigilance less frequently than expected.

Predictions 4a-b. For neighboring group calls, the observed response rates for adult males with odds for and against the focal group were not significantly different than expected based on chance (Chi-square test: $\chi^2=1.62$; $p=0.20$; Fig. 9). In response to neighboring group calls, observed vigilance rates in adult females with infants when numeric odds were for or against the focal group were not significantly different than expected based on chance (Chi-square test: $\chi^2=0.79$; $p=0.37$; Fig. 10).

Discussion

Both male and female *A. palliata* at Rancho Manacal display evidence of participation in intergroup encounters. They show a greater interest in intergroup bouts than intragroup calls or calls made in response to other noises (i.e., “other” calls). When comparing intragroup to other calls, however, females responded at a higher rate to intragroup calls and males responded at a higher rate to other calls. Other calls were typically elicited by trucks and heavy machinery or thunder, which were much louder than the monkey howls. Similar findings have been documented in closely related black howler monkeys (*A. pigra*; Horwich and Gebhard 1983). In this study, male response can be explained in the context of territory defense: these noises represent a potential territory invasion. Similarly, males at Rancho Manacal could exhibit relatively high response rates to other calls as compared to those produced during intragroup howling bouts due to territory defense. Females, on the other hand, have no interest in territory defense; therefore, they exhibit higher response rates to intragroup calls, which may serve as a warning to possible intrusions by extra-group males.

Both sexes usually participated in intergroup encounters more often when the encounter represented a “riskier” one (i.e., situations in which a potential fitness cost was at stake). In other words, although males participated in intergroup encounters in general, they were more likely to respond when there were more adult females in the group. Interestingly, males were not more likely to respond when there was a high ratio of infants in the group. Similarly, females with infants paid attention to male loud calls more than females without infants. In both cases, animals at risk of reduced fitness, either in the form of reproductive opportunity or reproductive investment, responded at a higher rate than expected. Intergroup loud calls represent potential group takeovers, and whether or not a group male’s infant is killed during a takeover is insignificant because he can easily sire more offspring. Thus, infant presence is irrelevant to males. Male fitness is greatly influenced by access to female mates. Intergroup howling may deter extra-group males from entering and monopolizing access to group females. For females, infant presence is an important factor contributing to intergroup encounter participation. A female with an infant has invested many resources throughout gestation and lactation. Therefore, the loss of an infant would cause a much greater loss to female than to male fitness. I was surprised to find that males did not use infants to determine their rate of participation. On the one hand, it may be that infanticide is not a strong selective agent in this population (as it has never been observed in over X years of observation). However, our data from females run counter to this hypothesis. On the other hand, perhaps infanticide is rare enough that it has not selected for counterstrategies in males yet has selected for behavioral vigilance (possibly one form of counterstrategy) in females.

Both males and females responded to intergroup calls significantly more when they originated from neighboring groups than from more distant groups. Not only does

this provide evidence that animals participated in intergroup encounters during risky situations, but it also suggests that, while rarely observed, group takeovers are an important selective force for animals at Rancho Manacal. Being aware of the origin of intergroup loud calls and the potential that they represent a reproductive threat is adaptive; therefore, response to these particularly risky situations may be associated with higher rates of overall fitness.

Intergroup participation of neither males nor females was affected by numeric odds. A similar study conducted on *A. pigra* indicated that howling responses were strongest when males faced favorable odds (Kitchen 2004). Subjects of my study were also expected to participate at higher rates when group males outnumber neighboring males because group males would have an advantage if they encounter were to become physical. Because monkeys Rancho Manacal live at such high densities, they likely “know” the neighboring groups quite well and remember the outcomes of previous encounters. The Kitchen (2004) study used calls from unknown individuals using a playback experimental design. Therefore, it remains possible that this population *could* possibly use numeric odds to determine participation if the calls were from an unknown group. However, observational analyses alone were not able to tease this apart. Furthermore, for intergroup encounters with known males, it remains likely that factors such as dominance and individual reputation may play a stronger role in predicting the outcome. Thus, in sum, a *solely* numerical analysis such as numeric odds does not explain participation in intergroup encounters at Rancho Manacal.

Overall, the results of this study suggest that intergroup encounters at Rancho Manacal function within a collective action framework. Individuals at the greatest risk of fitness loss participate; and, for the most part, they do so most often when group takeovers are a true threat. This is consistent with intergroup behavior in encounters across primate species (e.g., Kitchen and Beehner 2007). Nevertheless, male loud calling can also be explained in at least two other way. First, howling could be used to maintain intergroup spacing as described in cercopithecines (Byrne 1982) and gibbons (*Hylobates* spp., Cowlshaw 1992). However, this does not explain why females exhibit an interest in male loud calls at such high rates in potentially costly situations. Alternatively, male loud calls could simply be sexually selected signals that display competitive ability to other males (Kitchen and Beehner 2007) and potential mates (Delgado 2006). This could explain why females respond to intragroup calls more than other calls: they have an interest in acquiring more mates. However, because of high response rates exhibited by females with infants, the possibility of infanticide in this population suggests that extra-group males would actually be a very poor choice of mate. Therefore, collective action remains the best explanation for intergroup encounters at Rancho Manacal.

Several limitations were noted throughout this study. First, because female *A. paliatta* do not produce loud calls, I had to use vigilance as a proxy for intergroup encounter participation. While vigilance does signify interest in a stimulus, it is only visible to intra-group animals. Individual identification was not possible because at Operation Wallacea, research assistants volunteer for as few as one week at each research site. With eight groups as large as 45 animals, it would be difficult for even the professional guides to recognize individual animals. That being said, not knowing individuals contributed to the remainder of my research limitations. A lack of genetic information created a problem of pseudoreplication. I had to assume that each call was

independent when in reality, many calls from the same group were produced by the same one or two, likely dominant, males. Knowing dominance relationships would have allowed me to test whether alpha males, which receive priority access to mating, were more strongly affected by numeric odds or the infant-male ratio. This would have provided more insight into the possibility of infanticidal group takeovers. Genetics would also have been useful in determining infant age, or how much of an investment it represented to the infant's mother. A lack of hormonal analysis made it nearly impossible to know a female's reproductive state, particularly whether adult females without infants were in the early stages of pregnancy (and would have a stake in keeping extra-group males from entering the group) or cycling (and would be relatively unaffected by the arrival of an extra-group male). Finally, *A. palliata* are typically characterized by bisexual dispersal, but whether the same patterns exist in such densely populated forest fragments is unknown. If both sexes do disperse, it would have been interesting to test how recent immigrants and individuals who had not yet dispersed from their natal group respond to intergroup encounters.

Future directions include learning individuals for at least some groups at Rancho Manacal, acoustic analysis of loud calls, and comparing rates of intergroup encounters across *Alouatta* populations, especially for different population densities. Testing these patterns would help contribute to a better understanding of how wild primates respond to collective action problems.

References

- Altmann J. 1974. Observational study of behaviour: sampling methods. *Beh* 49:227-267
- Barton RA, Byrne RW, Whiten A. 1996. Ecology, feeding competition and social structures in baboons. *Behavioral Ecology and Sociobiology* 38:321-329
- Byrne RW. 1982. Primate vocalisations: Structural and functional approaches to understanding. *Behav* 80: 241–258
- Carpenter CR. 1934. A field study of the behavior and social relations of howling monkeys (*Alouatta palliata*). *Comp Psychol Monogr* 10:1 – 168
- Chapman CA, Balcomb SR (1998) Population characteristics of howlers: ecological conditions or group history. *Int J Primatol* 19:385-403
- Cheney DL. 1981. Intergroup encounters among free-ranging vervet monkeys. *Fol Primatol* 35:124-146
- Clarke MR (1983) Infant-killing and infant disappearance following male takeovers in a group of free-ranging howling monkeys (*Alouatta palliata*) in Costa Rica. *Am J Primatol* 5:241-247
- Cristobal-Azkarate J, Arroyo-Rodriguez V. 2007. Diet and activity patterns of howler monkeys (*Alouatta palliata*) in Los Tuxtlas, Mexico: effects of habitat fragmentation and implications for conservation. *Am J Primatol* 69:1-17
- Crockett CM, Eisenberg JF. 1987. Howlers: variations in group size and demography. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, ed., *Primate societies*. Chicago: University of Chicago Press. pp 54–68
- Cowlshaw G. 1992. Song function in gibbons. *Behaviour* 121: 131–153
- Delgado RA. 2006. Sexual selection in the loud calls of male primates: signal content and function. *Int J Primatol* 27:5-25
- Glander KE (1992) Dispersal patterns in Costa Rican mantled howling monkeys. *Int J Primatol* 13:415–436
- Gautier JP, Gautier G. 1977. Communication in old world monkeys. How animals communicate. pp 890-964
- Hamilton, WD (1964) The genetical evolution of social behaviour. *J Theor Biol* 7:1-16
- Hershkovitz P. 1949. Mammals of northern Colombia. Preliminary report No. 4: monkeys (primates), with taxonomic revisions of some forms. *Proc US Nat Hist Mus* 98:323-427
- Horwich R, Gebhard K. Roaring rhythms in black howler monkeys (*Alouatta pigra*) of Belize. *Primates* 24:290-296
- Hrdy SB. 1977. Infanticide as a male reproductive strategy. *Am Sci* 65: 40-49
- Jolly A. 1966. *Propithecus verreauxi*. In: Jolly A, ed., *Lemur behavior*. Chicago: The University of Chicago Press.
- Kitchen DM. 1996. 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. *Am J Phys Anthropol* 131:73-83
- Kitchen DM, Beehner JC. 2007. Factors affecting individual participation in group-level aggression among non-human primates. *Behav* 144:1551-1581
- Lazaro-Perea C. 2001. Intergroup interactions in wild common marmosets, *Callithrix jacchus*: territorial defence and assessment of neighbors. *Animal Behav* 62:11-21

- Maynard Smith J, Parker GA. 1976. The logic of asymmetric contests. *Animal Behav* 24:159-175
- Milton K. 1980. *The Foraging Strategy of Howler Monkeys; A Study of Primate Economics*, Columbia University Press, New York
- Nunn, CL. 2000. Collective benefits, free-riders, and male extra-group conflict. In: Kappeler PM, ed., *Primate Males: Causes and Consequences of Variation in Group Composition*. Cambridge: Cambridge University Press. pp 192-204
- Perry S. 1996. Intergroup encounters in wild white-faced capuchins (*Cebus capuccinus*). *Int J Primatol* 17:309-330
- Preuschoft S, van Schaik CP. 2000. Dominance and communication. In: Aureli F, de Waal FBM (eds) *Natural conflict resolution*. University of California Press, Berkeley, pp 77-105
- Ryan SJ, Starks PT, Milton K, Getz WM. 2008. Intersexual conflict and group size in *Alouatta palliata*: a 23-year evaluation. *Int J Primatol* 29:405-420
- Sicotte P. 1993. Intergroup encounters and female transfer in mountain gorillas – influence of group composition on male-behavior. *Am J Primatol* 30:21-36
- Sekulic R, Chivers DJ. 1986. The significance of call duration in howler monkeys. *Int J Primatol* 7:183-190
- Seyfarth RM, Cheney DL, Bergman T, Fischer J, Zuberbuhler K, Hammerschmidt K. 2010. The central importance of information in studies of animal communication. *Animal Behav* 80:3-8
- Struhsaker TT. 1975. *The red colobus monkey*. University of Chicago Press, Chicago
- Trivers RL. 1972. Parental investment and sexual selection. In: Campbell B ed. *Sexual selection and the descent of man*. Aldine, Chicago:136-179
- Ydenberg RC, Giraldeau L-A, Falls JB. 1988. Neighbors, strangers, and the asymmetric war of attrition. *Anim Behav* 37:336-337

Tables and Figures

Table 1. Group composition ranges for 2009-2012.

Group Number	Number of Adult Males	Number of Adult Females	Number of Infants	Total Group Size
1	3 – 4	8 – 12	1 – 3	15 – 21
2	4	8 – 13	3 – 5	17 – 24
3	4 – 7	10 – 13	2 – 3	20 – 24
4	6 – 10	9 – 20	6 – 7	29 – 40
5	3 – 6	8 – 14	3 – 5	17 – 24
6	9 – 11	12 – 21	6 – 10	35 – 45
7	3 – 4	8 – 10	1 – 3	14 – 19
8	5 – 8	10 – 19	5 – 10	25 – 39

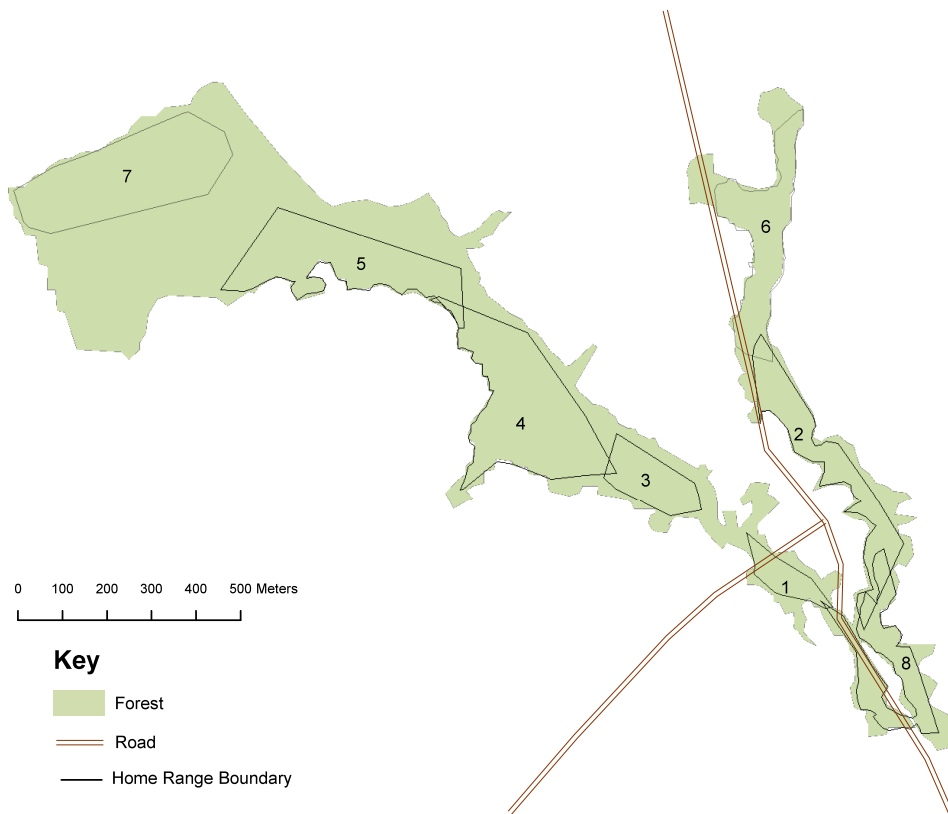


Figure 1. Home range map for eight *Alouatta palliata* groups at Rancho Manacal, Honduras. Solid lines indicate home ranges for each of the numbered groups.

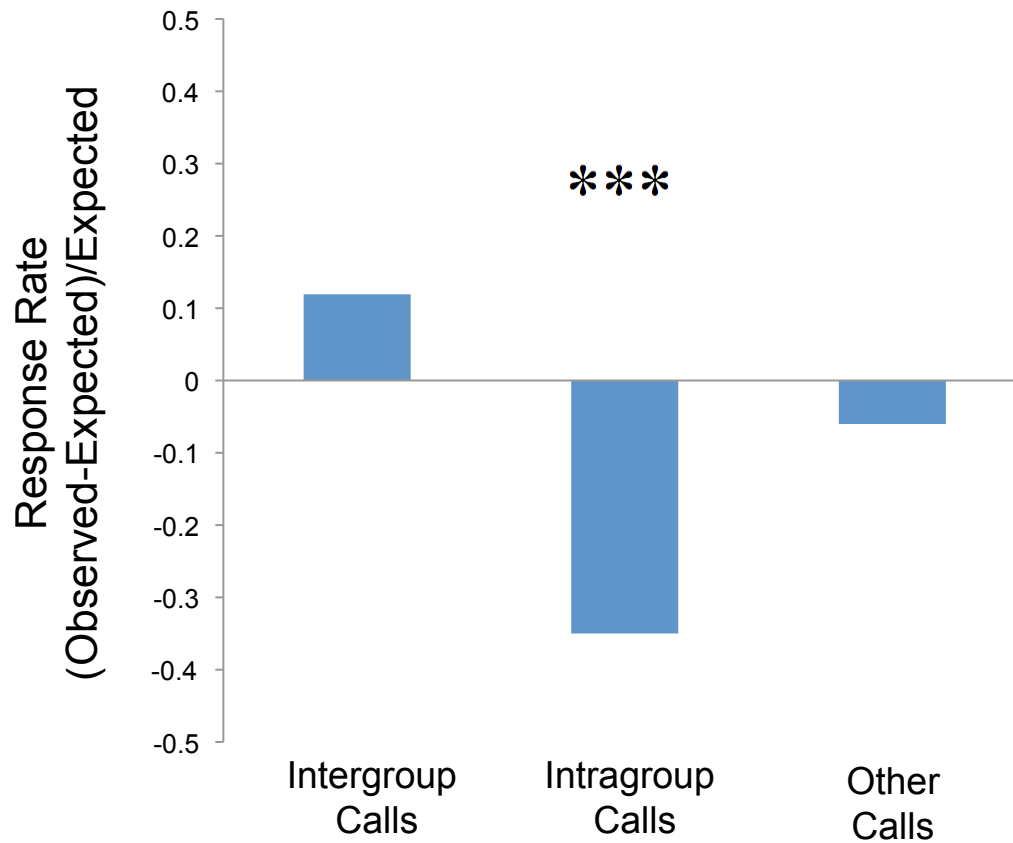


Figure 2. Adult males responded significantly more frequently to intergroup than to intragroup or other calls, with a higher response rate for other calls than intragroup calls (Chi-square test: $\chi^2 = 242.87$; $p < 0.001$).

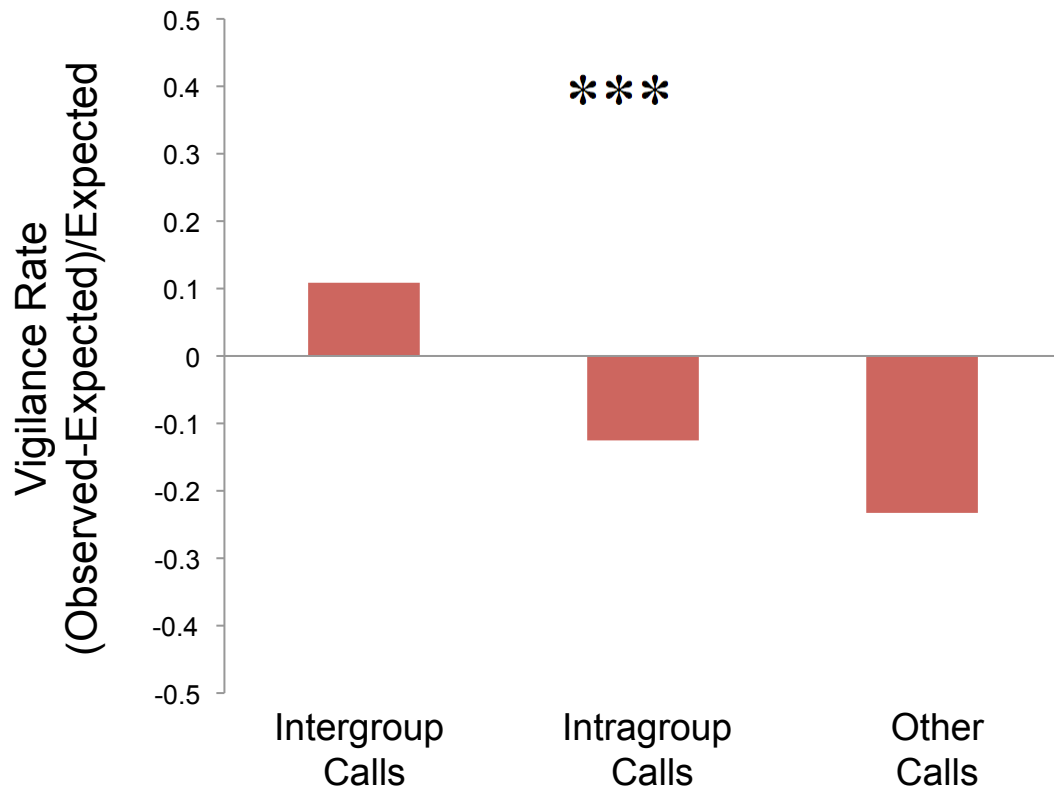


Figure 3. Adult females responded significantly more frequently to intergroup than to intragroup or other calls, with a higher vigilance rate for intragroup than other calls. (Chi-square test: $\chi^2=82.22$; $p<0.001$).

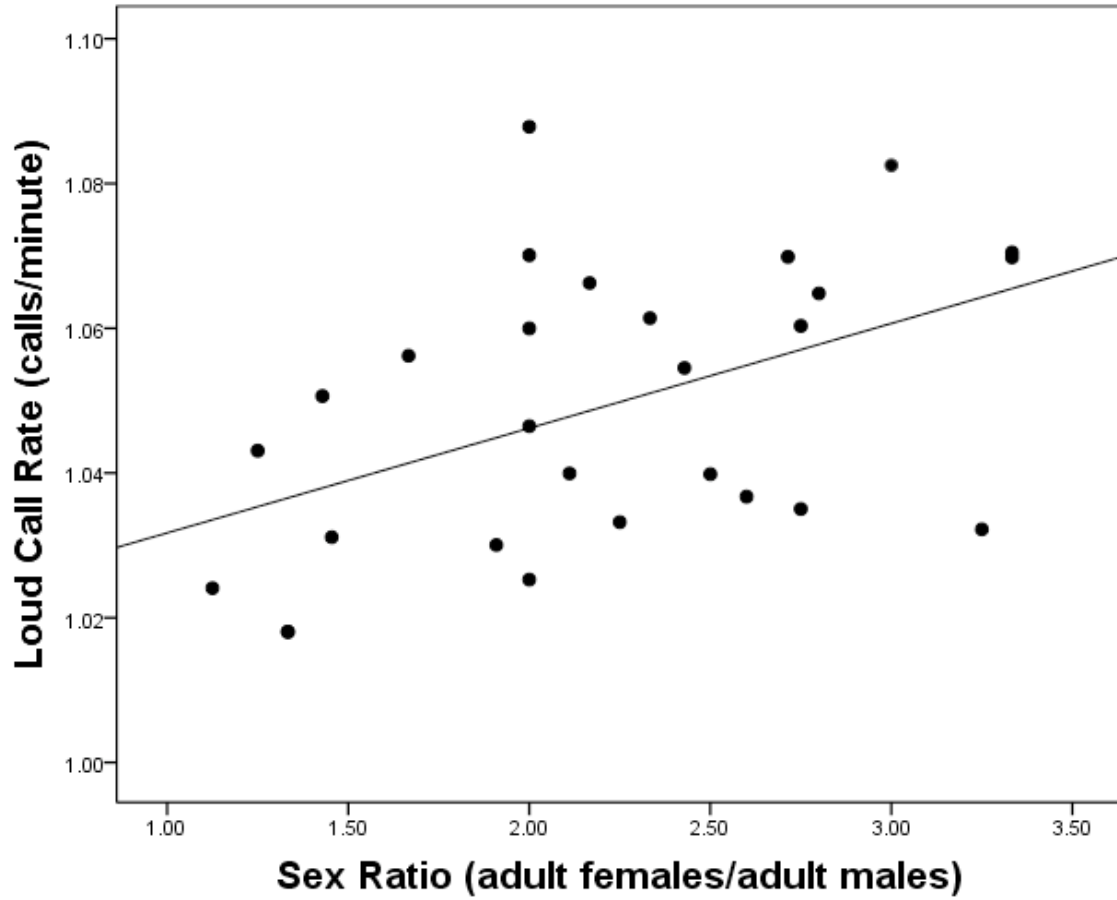


Figure 4. Adult male loud call rate (calls/minutes) increased with sex ratio (adult females/adult males) (Linear regression; $R=0.23$; $p=0.01$).

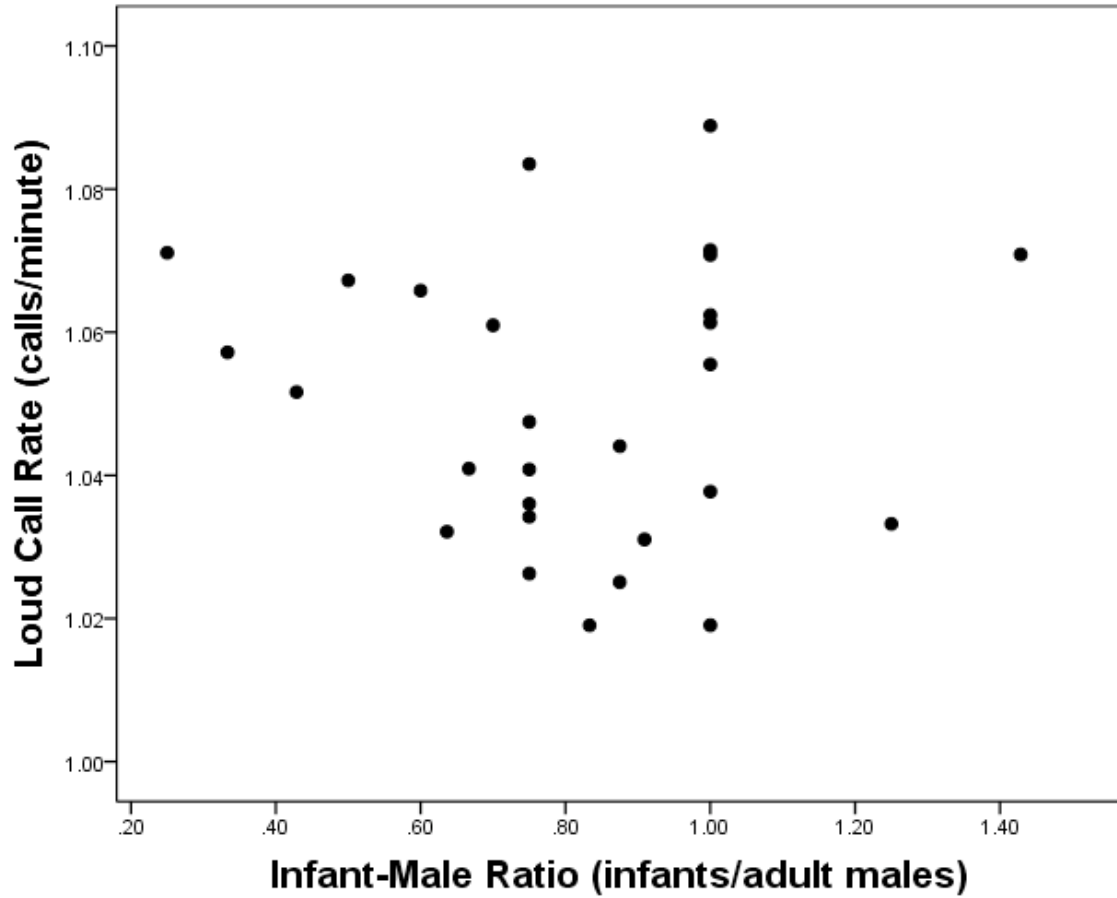


Figure 5. Relationship between infant-male ratio (number infants/number adult males) and adult male loud call rate (number calls/minute) (Linear regression; $R < 0.05$; $p = 0.83$).

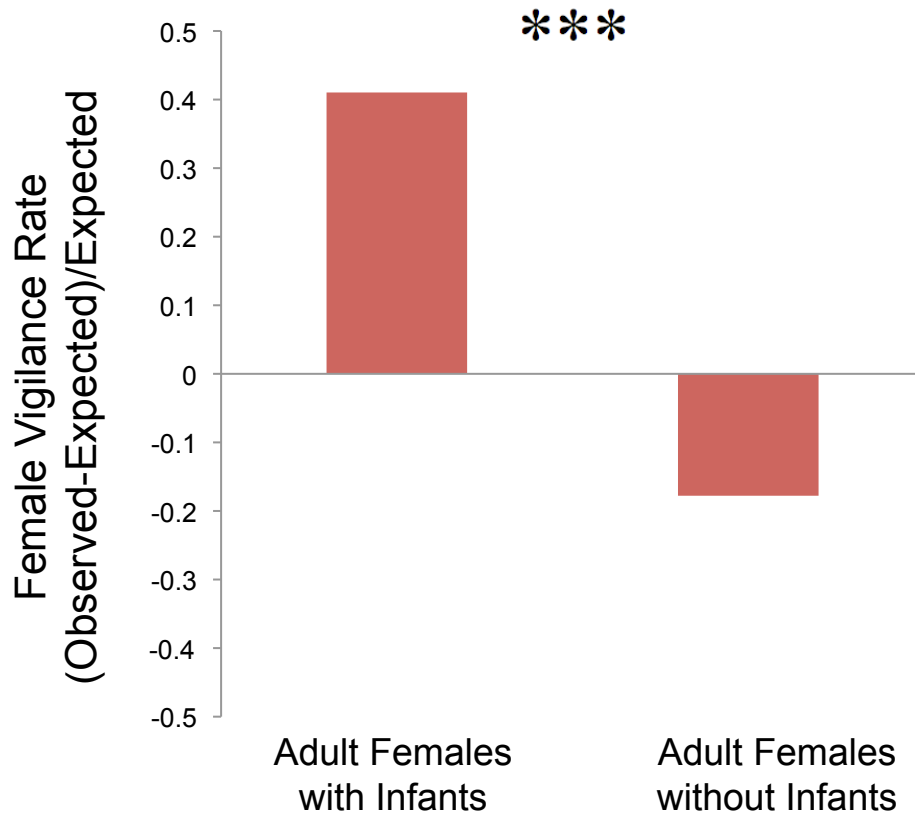


Figure 6. Adult females with infants exhibited vigilance significantly more frequently than did adult females without infants in response to all male loud calls (Chi-square: $\chi^2=294.00$; $p<0.001$).

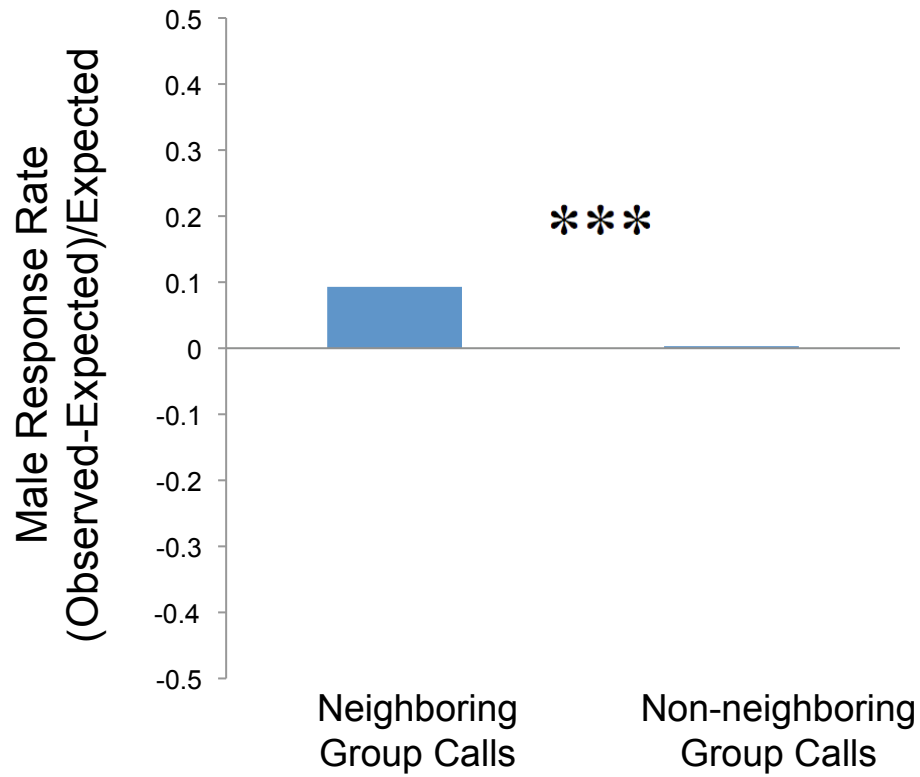


Figure 7. Adult males responded significantly more frequently to neighboring group loud calls than to non-neighboring group loud calls (Chi-square test: $\chi^2=21.37$; $p<0.001$).

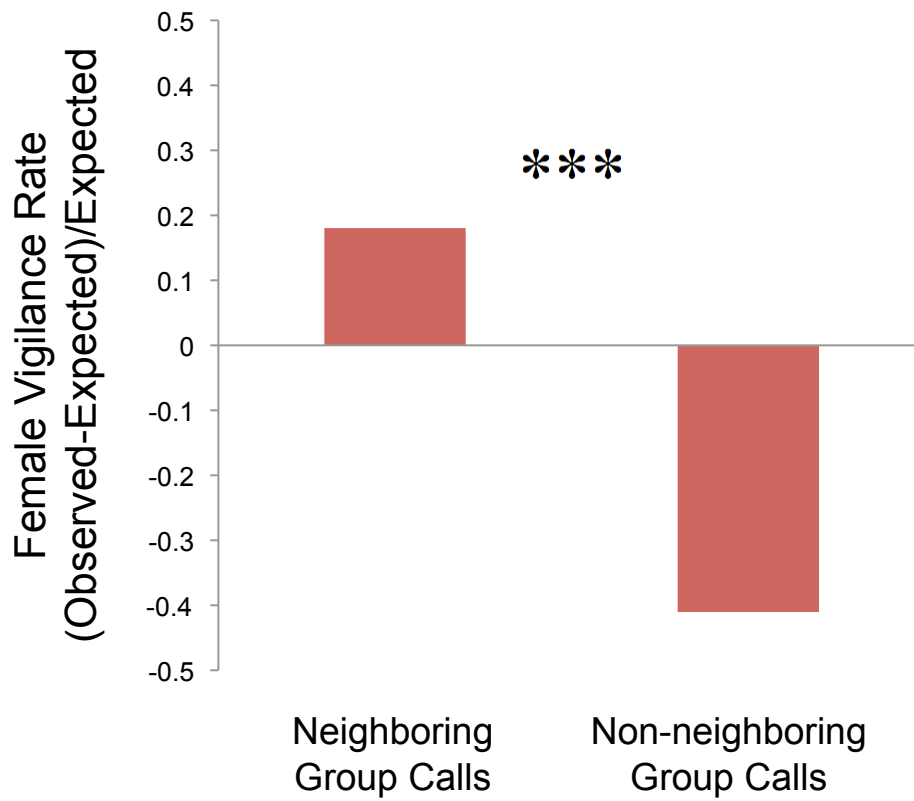


Figure 8. Adult females with infants exhibited vigilance more frequently in response to neighboring group male loud calls than to non-neighboring group male loud calls (Chi-square test: $\chi^2=55.20$; $p<0.001$).

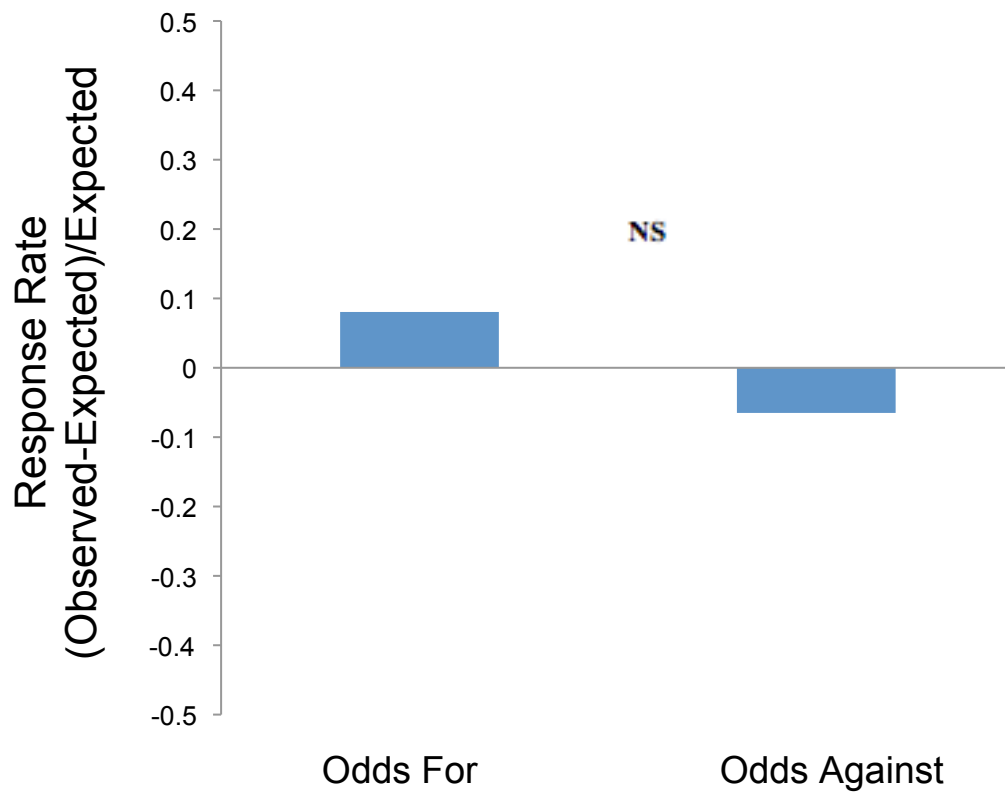


Figure 9. For neighboring group calls, male response rate was not significantly different when numeric odds were “for” (i.e., neighboring group had fewer males than the focal group) or “against” (i.e., neighboring group had more males than the focal group; Chi-square test: $\chi^2=1.62$; $p=0.20$).

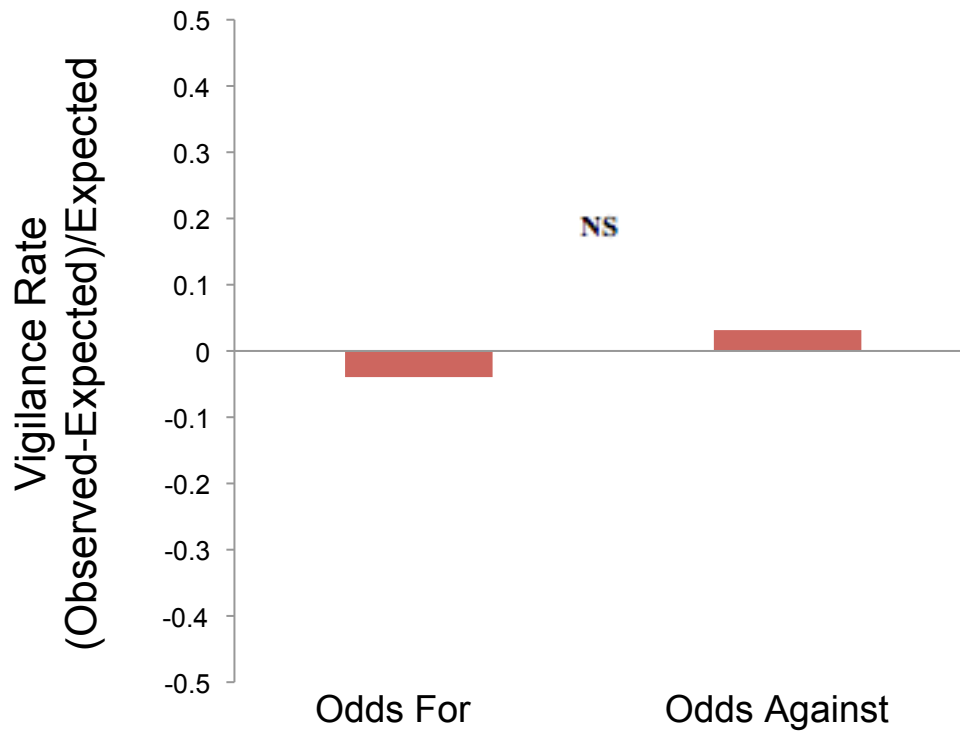


Figure 10. Vigilance rates to neighboring group calls for adult females with infants were not significantly different when numeric odds were “for” (i.e., neighboring group had fewer males than the focal group) or “against” (i.e., neighboring group had more males than the focal group; Chi-square test: $\chi^2=0.79$; $p=0.37$).

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