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RESEARCH ARTICLE

"Dear Enemies", "Nasty Neighbors", and the Strength in Numbers: Exploring the Behavioral and Hormonal Responses of Mantled Howler Monkey Males to Simulated Intruder Loud Calls

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ABSTRACT

Loud calls are critical for primate intergroup communication, influencing resource defense, territorial boundaries, and conflict management. This study examined the interplay of familiarity and numeric odds in shaping the behavioral and hormonal responses of male mantled howler monkeys (*Alouatta palliata*) to simulated intruder calls. Using playback experiments, we tested whether responses were consistent with "dear enemy" dynamics, which predict stronger responses to unfamiliar intruders, or "nasty neighbor" dynamics, which predict stronger responses to familiar intruders. Additionally, we assessed the influence of numeric odds, hypothesizing stronger responses under favorable conditions. Behavioral responses, including vocalization and approach latencies, were primarily influenced by numeric odds, with shorter latencies observed under favorable odds. Vocal duration, however, was longer when intruders were familiar, consistent with "nasty neighbor" dynamics. Hormonal responses, measured via fecal glucocorticoid and testosterone metabolites, increased in response to unfamiliar intruders, supporting "dear enemy" predictions. Interaction effects showed that familiarity modulated approach duration and latency when numeric odds were unfavorable. These findings reveal the distinct roles of numeric odds and familiarity in shaping immediate and prolonged responses to intruders. Numeric odds influenced engagement decisions, while familiarity was related to stress-related hormonal changes and vocal communication strategies. This study contributes to the understanding of intergroup dynamics by clarifying the role of competitive asymmetries and social relationships in conflict management. Future work incorporating multimodal cues and ecological variability will further elucidate the adaptive significance of these responses.

1 | Introduction

Some primate vocal signals are high amplitude and low frequency. Such "loud calls" are known to be produced by several primate species (Delgado 2006; Mitani and Stuht 1998; Wich and Nunn 2002). These calls are audible over long distances (e.g., 3 km in siamangs, *Symphalangus syndactylus*: Chivers 1976), and convey information to listeners on the location (e.g., Mitani 1985; Wich et al. 2002), direction of movement (i.e., approach/retreat: Whitehead 1987), identity (e.g., Clink et al. 2017; Owren and Rendall 2003; Semple et al. 2009; Terleph et al. 2015), and sex (e.g., Ammie 2019; Garcia de la Chica et al. 2020) of callers.

Abbreviations: fGCM, fecal glucocorticoid metabolites; fTM, fecal testosterone metabolites.

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Summary

- Under favorable numeric odds mantled howler monkey males vocalize toward and approach intruders more quickly, reflecting strategic engagement based on conflict success likelihood.
- Vocal durations are longer toward familiar intruders, aligning with "nasty neighbor" dynamics, while hormonal responses to unfamiliar intruders indicate stress and unpredictability, supporting "dear enemy" dynamics.
- Numeric odds primarily affect immediate engagement decisions, whereas familiarity modulates vocal strategies and hormonal adjustments, revealing adaptive conflict management in mantled howler monkeys.

Amongst males, the acoustic attributes of loud calls vary with the size, dominance rank, and age of the individual producing them (e.g., Barelli et al. 2013; Benítez et al. 2017; Ey et al. 2007; Fischer et al. 2002; Kitchen et al. 2003; Neumann et al. 2010), suggesting that these vocalizations may be honest signals of the competitive potential of callers.

Individuals face a range of trade-offs when responding to vocalizations from neighboring groups or intruders. Theoretical models, such as the "dear enemy" and "nasty neighbor" effects, have been proposed to explain the variation in these responses. The "dear enemy" effect suggests that individuals may reduce aggression toward familiar neighbors because they pose a lower risk to territorial stability than unfamiliar intruders (Temeles 1994; Ydenberg et al. 1988). In contrast, the "nasty neighbor" effect posits that familiar neighbors can be a greater threat than strangers, especially in resource-rich environments, leading to more aggressive responses to nearby rivals (Müller and Manser 2007). However, numeric odds (i.e., the relative difference in group sizes or the number of individuals available to participate in a conflict) are critical in shaping these interactions (McComb et al. 1994). Studies across diverse taxa illustrate that individuals often escalate aggression when they hold a numeric advantage. For example, spotted hyenas (*Crocuta crocuta*) and chimpanzees (*Pan troglodytes*) show greater willingness to approach and vocalize when their groups outnumber potential intruders (Benson-Amram et al. 2011; Wilson et al. 2012). Similarly, tufted capuchin monkey (*Sapajus nigritus*) groups are more likely to engage in resource defense when they have more males than their competitors, as the probability of winning encounters increases with numeric superiority (Scarry 2020). Conversely, when groups are at a numeric disadvantage, retreat, and reduced aggression are common strategies to avoid high costs of escalated conflict (Beehner and Kitchen 2007). These examples highlight the interplay of familiarity, numeric odds, and ecological context in shaping territorial responses, providing a framework for understanding how animals manage territories and intergroup competition.

Howler monkeys (*Alouatta* spp.) are ideal models for studying the role of loud calls in territorial behavior. Their powerful, low-frequency calls, audible over 1 km in dense tropical forests (Baldwin and Baldwin 1976), may be energetically costly to produce but serve critical social and ecological functions, including resource defense, intergroup spacing regulation, and avoidance of physical confrontations (e.g., Byrne and da Cunha 2006; Grassetto et al. 2007; Hopkins 2013; Kitchen 2004; Maya-Lastra et al. 2023; Sekulic 1982; Van Belle and Estrada 2019). The acoustic attributes of loud calls encode information on the body size of callers (De los Santos-Mendoza and Van Belle 2024), which males use to adjust their behavioral and hormonal responses (Maya-Lastra et al. 2024). Intergroup interactions in howler monkeys may follow "dear enemy" dynamics, as groups often show reduced aggression toward familiar neighbors, presumably to minimize the costs of repeated conflicts with groups they encounter frequently (Ceccarelli et al. 2021). However, responses to neighboring calls can vary depending on the social and ecological context. For example, Hopkins (2013) found that mantled howler monkeys (*A. palliata*) were more likely to approach howling neighbors higher in the dominance hierarchy than those lower down, potentially reflecting priority of access to higher-quality resources by dominant groups. That study also noted that numeric odds did not significantly predict spatial responses in groups with established interaction histories. This suggests that among familiar neighbors, dominance relationships, rather than sheer numbers, may be more salient indicators of competitive ability. Nevertheless, playback studies have shown that howler monkeys are more likely to approach intruders when they perceive a numeric advantage (Kitchen 2004; Maya-Lastra et al. 2024) or at even odds in the context of naturally occurring intergroup encounters (Van Belle and Scarry 2015). These findings highlight the importance of considering both contextual factors and methodological approaches when interpreting intergroup interactions and vocal behaviors in howler monkeys.

In this study, we conducted playback experiments to investigate how familiarity with neighboring groups and numeric odds influence the behavioral and hormonal responses of mantled howler monkey males to intruders. We hypothesized that if "dear enemy" dynamics are the main driver of male responses, they would respond more aggressively, with shorter latencies (i.e., time to first response) and longer durations of approaches and vocalizations, when faced with calls from unfamiliar than familiar intruders, independently of numeric odds. Conversely, if numeric odds are the main factor for male behavior, stronger responses (i.e., shorter latencies and longer durations of approaches and vocalizations) would occur in the context of favorable than equal or unfavorable numeric odds. To explore the physiological underpinnings of male responses to playbacks, we measured fecal glucocorticoid (fGCM) and testosterone (fTM) metabolite concentrations. We expected increased fGCM and fTM concentrations in the most challenging contexts (i.e., interactions with unfamiliar intruders or unfavorable numeric odds), reflecting elevated physiological stress and heightened territorial motivation, respectively (Dias et al. 2022).

2 | Methods

2.1 | Ethical Note

The study followed the Code of Best Practices for Field Primatology provided by the International Primatological Society and the American Society of Primatologists, as well as the American Society of Primatologists Principles for the Ethical

Treatment of Nonhuman Primates. We complied with the Mexican Law and research protocols were approved by permits SGPA/DGVS/13528/19 and SGPA/DGVS/04015/21 from Secretaria de Medio Ambiente y Recursos Naturales, Mexico.

2.2 | Study Site and Subjects

The study was conducted on four groups of mantled howler monkeys, comprising 11 adult males, living in two forest fragments within the Los Tuxtlas Biosphere Reserve (Veracruz, México; Table 1). These groups, which have been monitored extensively over several years (Rangel Negrín et al. 2021), were habituated to the presence of researchers. We recognized males through distinctive physical features, including yellow fur patches on tails and feet, scars, and unique facial characteristics.

2.3 | Playback Stimuli

We recorded spontaneous loud calls from adult males in six groups, using a Sennheiser MKE600 directional microphone and a Marantz PMD660 digital recorder. These recordings ($n = 65$) consisted of complete loud calling bouts (barks and roars) free of background noise, classified as vocalization types A1 and C1, following Baldwin and Baldwin (1976). We modified the number of individuals vocalizing in each recording, from both known (i.e., groups residing in the same habitat as the study groups) and unknown (i.e., groups residing in a different forest fragment > 20 km from the study groups) groups to examine numeric odds effects (Kitchen 2004; Van Belle and Scarry 2015). This was accomplished by using Adobe Audition's (version 12.1.4.5) multitrack option to overlap vocalizations from different males until the desired number of males was reached. In this way, six treatments were obtained: unknown groups with higher, lower, and equal numbers of individuals than the experimental group; known groups with higher, lower, and equal numbers of individuals than the experimental group. All vocalization packets obtained had a mean (± SD) duration of 5 ± 0.007 min (range = 4:40–5:19; Kitchen 2004). The 5-min duration was determined during pilot testing because when a spatial response to the simulated vocalizations occurred, individuals reached the speaker within an average of 5 min.

2.4 | Playback Design and Behavioral Data Collection

Between March 2020 and December 2021, we ran three trials per treatment per group, with an intertrial median interval of 7 days (range: 2–14 days; $n = 72$ trials). Trial order was randomized. Trials commenced post-feeding when all adult males were resting, no loud calls from other groups were heard for a least 30 min, and there were no salient anthropogenic stimuli (e.g., people walking by the group, anthropogenic noise). A Bose 151SE speaker, positioned 100 m from the nearest subject and raised on an 8-m fiberglass pole, broadcasted the playbacks via a JBL A6002 amplifier powered by a 12V/7A Powersonic PS-1270 F2 battery and controlled by a Motorola Moto E5 Play phone. We always placed the speaker inside the focal group's home range to simulate actual intrusion.

For each trial, we conducted a 1-h focal animal sampling (Altmann 1974) with the first male to vocalize or move. We recorded approaches as movements > 1 m within 45° in the direction of the speaker.

2.5 | Fecal Sample Collection and Hormonal Analysis

To assess hormonal responses of males to playbacks, we collected fecal samples on trial days (baseline) and the following day (response) to account for the ~24-h excretion delay of steroid hormones following stimulation (Aguilar-Cucurachi et al. 2010; Cañadas-Santiago et al. 2020). We collected a total of 174 fecal samples (mean ± SD: 8 ± 2 samples per male) immediately post-defecation and stored them on ice in labeled polyethylene bags before freezing at −20°C. We dried feces in an oven (Cole-Parmer OVG-400–56-120 Gravity Convection Drying Oven) at 60°C and extracted steroids following a modification of the method by Wasser et al. (2000). Briefly, we shook 0.6 g of homogenized, dried, and pulverized feces for 30 min in 4.0-mL analytical-grade methanol. We centrifuged extracts (460 g for 30 min) and recovered the supernatant. After complete evaporation of the solvent in a water bath at 60°C for 24 h, we reconstituted pellets with 2-mL albumin buffer, which we used for assays. We determined fGCM and fTM concentrations in 174 samples with chemiluminescent immunoassays using commercial kits (Cortisol,

TABLE 1 | Attributes of study sites and groups.

Attribute	Group 1	Group 2	Group 3	Group 4
Site	Balzapote	Balzapote	La Flor de Catemaco	La Flor de Catemaco
Location	18°36′30.80″ N 95°04′ 15.69″ W	18°36′36.50″ N 95°04′ 11.16″ W	18°26′29.63″ N 95°03′ 01.75″ W	18°26′39.27″ N 95°03′ 08.88″ W
Fragment size (ha)	12	8	100	100
Groups	2	2	3	3
Adult males	2	2	3	4
Adult females	2	2	5	6
Juveniles	1	1	2	2
Infants	1	2	2	2

Immulite, Siemens; sensitivity = 5.5 nmol/L; calibration range = 28–1380 nmol/L; Testosterone, Immulite, Siemens; sensitivity = 0.5 nmol/L; calibration range = 0.7–55 nmol/L) and an automated immunoassay system (Immulite 1000 analyzer, Siemens). The antibodies in these kits are highly specific to cortisol and testosterone, showing low (< 9%) cross-reactivity with other compounds. Pooled fecal extracts, when added to standard curve points, exhibited similar slopes (fGCM: $R^2 = 0.95$, n = 8, $p < 0.001$; fTM: $R^2 = 0.88$, n = 8, $p < 0.001$), and serial dilutions of a fecal pool yielded results that were parallel to kits' standards (fGCM: $t = 0.9$, $n = 4$, $p = 0.402$; fTM: $t = 1.2$, $n = 4$, $p = 0.534$). For fGCM, intra-assay variation (coefficient of variation) averaged 7% ($n = 3$ samples), and inter-assay variation was 14% ($n = 4$ samples), whereas for fTM intra-assay variation was 3% ($n = 3$ samples) and inter-assay variation was 9% ($n = 4$ samples). These assays had been previously biologically validated (Cañadas-Santiago et al. 2020; Dias et al. 2022).

2.6 | Data Analysis

We analyzed four measures of the behavioral responses of males to playbacks: the latency to the first vocalization, the latency to the first approach (0–3600 s), the duration of vocalizations, and the duration of approaches (i.e., 0–3600 s). We used generalized linear models to analyze variation in these measures according to familiarity (categorical predictor, known/unknown caller), numeric odds (categorical predictor, against, even, and with odds), and the interaction between these predictors. We built models with negative binomial error distribution to account for overdispersion and logit link function.

We calculated variation in fGCM and fTM as the subtraction between baseline and response hormone concentrations per trial per male. We then assessed the influence of familiarity, numeric odds, and the interaction between these predictors on hormone variation with linear mixed models on log-transformed hormone values (after adding a constant, +1, to produce positive values). In these models, we included subject identity as a random factor to account for repeated sampling of males. We compared complete models (i.e., with fixed and random predictors) with a null model including only the random factor using likelihood ratio tests to determine whether the latter accounted for a greater proportion of the variation in the response variables than the former (Pinheiro and Bates 2000). We found significant differences ($p < 0.001$) in both comparisons, indicating that fixed predictors were more influential in the response variables than the random factor.

We added group identity as a control variable in all models to account for intergroup variation in several factors that were not assessed in our study but have been reported as influential in male behavior and endocrine function by previous research with howler monkeys. These include the presence of dependent infants (Kitchen 2004), food availability (Dias et al. 2022; Van Belle and Estrada 2019), location within the home range (Maya-Lastra et al. 2023), intergroup dominance relationships (Hopkins 2013), and the presence of solitary males (Cristóbal-Azkarate et al. 2006). We used Tukey contrasts as post-hoc tests in all models. Modeling was performed in R 4.3.0 (R Core Team 2024).

3 | Results

Males displayed vocal responses to all playbacks. The latency of vocal responses was influenced by numeric odds, with shorter latencies being displayed at odds with than at even and against odds (Table 2; Figure 1A; Tables S1 and S2), but neither familiarity nor its interaction with numeric odds was significant. Vocal duration was significantly influenced by familiarity with longer durations observed in the known condition (Figure 1B), while numeric odds and its interaction with familiarity were not significant.

Males approached the speaker on 69% of the playbacks. Latency to approach was influenced by numeric odds (Figure 1C) and its interaction with familiarity (Figure 1D), with shorter latencies observed at odds with. Regarding the interaction term, males called more quickly when numeric odds were favorable independently of familiarity, and when numeric odds were against if calls were from familiar intruders than in other conditions. Approach duration was significantly influenced by numeric odds (Figure 1E) and its interaction with familiarity (Figure 1F), with longer approaches observed in the odds with condition than in both odds even and odds against; and shorter approaches were recorded in the odds against from unknown callers and odds even from known callers than in all other conditions. Males had higher fGCM and fTM concentrations following playbacks from unknown than from known intruders (Figure 1G,H).

4 | Discussion

We examined the interplay between numerical odds and familiarity in shaping the behavioral and hormonal responses of male mantled howler monkeys to simulated intruder loud calls. Numerical odds influenced latency to vocalize and approach and duration of approach, while familiarity shaped vocal duration and hormonal responses. These patterns are consistent with the hypothesis that males adjust their responses based on the likelihood of success in encounters (numerical odds) and the perceived threat or predictability of intruders (familiarity). The divergence in behavioral and hormonal responses suggests adaptive strategies adjusted to immediate versus long-term intergroup dynamics, consistent with theoretical models of conflict and cooperation.

Behavioral responses were modulated by numeric odds and familiarity. Shorter latency to vocalize and approach under favorable odds supports evidence that individuals strategically engage when winning is likely (Benson-Amram et al. 2011; Furrer et al. 2011; McComb et al. 1994; Scarry 2020). These findings are consistent with general game theory principles and assessment models, which suggest that decision-making during conflicts is influenced by cost-benefit analyses based on group strength and potential rewards (Enquist and Leimar 1983; Maynard Smith 1974; Parker and

TABLE 2 | Generalized lineal and linear mixed model results (ANOVA) of the effects of familiarity with intruders and numeric odds on the behavior and hormone concentrations of male mantled howler monkeys exposed to simulated intruder loud calls (significant predictors in bold).

Variable/predictor	R^2[a]	χ^2	p
Latency to vocalization	0.70		
Familiarity		0.3	0.569
Numeric odds		**27.4**	**< 0.001**
Familiarity x numeric odds		4.6	0.102
Group		4.3	0.235
Duration of vocalization	0.50		
Familiarity		**16.7**	**< 0.001**
Numeric odds		1.2	0.554
Familiarity x numeric odds		2.0	0.372
Group		7.7	0.053
Latency to approach	0.67		
Familiarity		0.5	0.491
Numeric odds		**22.2**	**< 0.001**
Familiarity × numeric odds		**14.9**	**0.001**
Group		0.7	0.863
Duration of approach	0.47		
Familiarity		1.2	0.277
Numeric odds		**12.1**	**0.002**
Familiarity × numeric odds		**21.5**	**< 0.001**
Group		0.5	0.914
fGCM[b]	0.24 (0.24)		
Familiarity		**15.3**	**< 0.001**
Numeric odds		2.9	0.234
Familiarity × numeric odds		3.9	0.145
Group		0.9	0.819
fTM	0.23 (0.24)		
Familiarity		**13.1**	**< 0.001**
Numeric odds		4.1	0.132
Familiarity × numeric odds		3.0	0.218
Group		0.2	0.236

[a] In the fGCM and fTM models, the first value is the conditional coefficient of determination (R^2c), corresponding to the proportion of variance explained by the fixed factors, while the second (in parenthesis) is the marginal coefficient of determination (R^2m), corresponding to the proportion of variance explained by both the fixed and the random factors.

[b] fGCM are fecal glucocorticoid metabolites, and fTM are fecal testosterone metabolites.

Rubenstein 1981). Similarly, Kitchen (2004) demonstrated that alpha male black howler monkeys escalated their vocal and approach behaviors under favorable odds, particularly when young offspring were present, but avoided costly engagements when outnumbered. In contrast, Van Belle and Scarry (2015) found that black howler monkeys tended to engage under conditions of numerical parity, emphasizing the importance of maintaining competitive balance rather than clear dominance, which may reflect differences in intergroup dynamics compared to mantled howlers. Familiarity influenced vocal duration, with longer vocalizations directed toward familiar intruders, supporting the “nasty neighbor” effect, which posits that individuals exhibit stronger responses to familiar rivals who pose persistent and predictable threats (Godard 1993; Herbinger et al. 2009; Müller and Manser 2007; Olendorf et al. 2004). However, the stronger hormonal responses to unfamiliar intruders (discussed below) reflect elements of the “dear enemy” effect, in which individuals prioritize responding to less predictable, potentially dangerous unfamiliar rivals (Fisher 1954; Ydenberg et al. 1988).

Hormonal responses were influenced by familiarity but not by numerical odds. Unfamiliar intruders elicited higher glucocorticoid and testosterone concentrations, consistent with the “dear enemy” effect, which suggests that individuals perceive novel rivals as unpredictable and potentially more threatening (Getty 1987; Kitchen 2004; Mirville et al. 2018; Rendall et al. 1996; Sapolsky 1992; Scarry 2020). These hormonal responses may also reflect heightened activity (e.g., vigilance, movement) and physiological preparation for potential escalation (Kurihara and Muto 2021), consistent with studies in other taxa where unpredictability affects physiology (Sapolsky 2005, 2021; Wingfield et al. 1990). The lack of numerical odds effects on hormonal responses suggests a decoupling between immediate behavioral decisions and physiological states. While numeric odds influence the likelihood of engaging in physical or vocal interactions, hormonal responses are more likely to reflect the perceived long-term risk or unpredictability of a rival (Watts and Mitani 2001; Wich and Nunn 2002).

This study addresses a limitation of previous work that could not disentangle the relative effects of numerical odds and familiarity due to methodological constraints (Ceccarelli et al. 2021). By systematically isolating these factors through playback experiments, we show that numeric odds primarily affect immediate behavioral responses (latency to vocalize and approach), while familiarity affects vocal duration and hormonal responses. These results also complement previous research on other populations of mantled howler monkeys (Hopkins 2013), which documented variability in intergroup behavior but did not explicitly analyze the relative influence of familiarity and numerical odds. Furthermore, our results are consistent with findings in black howler monkeys, in which familiarity influenced navigational decisions and vocal behaviors during intergroup encounters (Kitchen 2004). However, black howler monkey groups showed a stronger tendency to engage with nearby rivals regardless of familiarity, which may reflect interspecific differences in social systems or the intensity of intergroup competition (Ho et al. 2014; Van Belle and Bicca-Marques 2015). Comparisons with studies of other species further underscore the importance of numerical odds. These studies found that group size asymmetries are critical determinants of engagement,

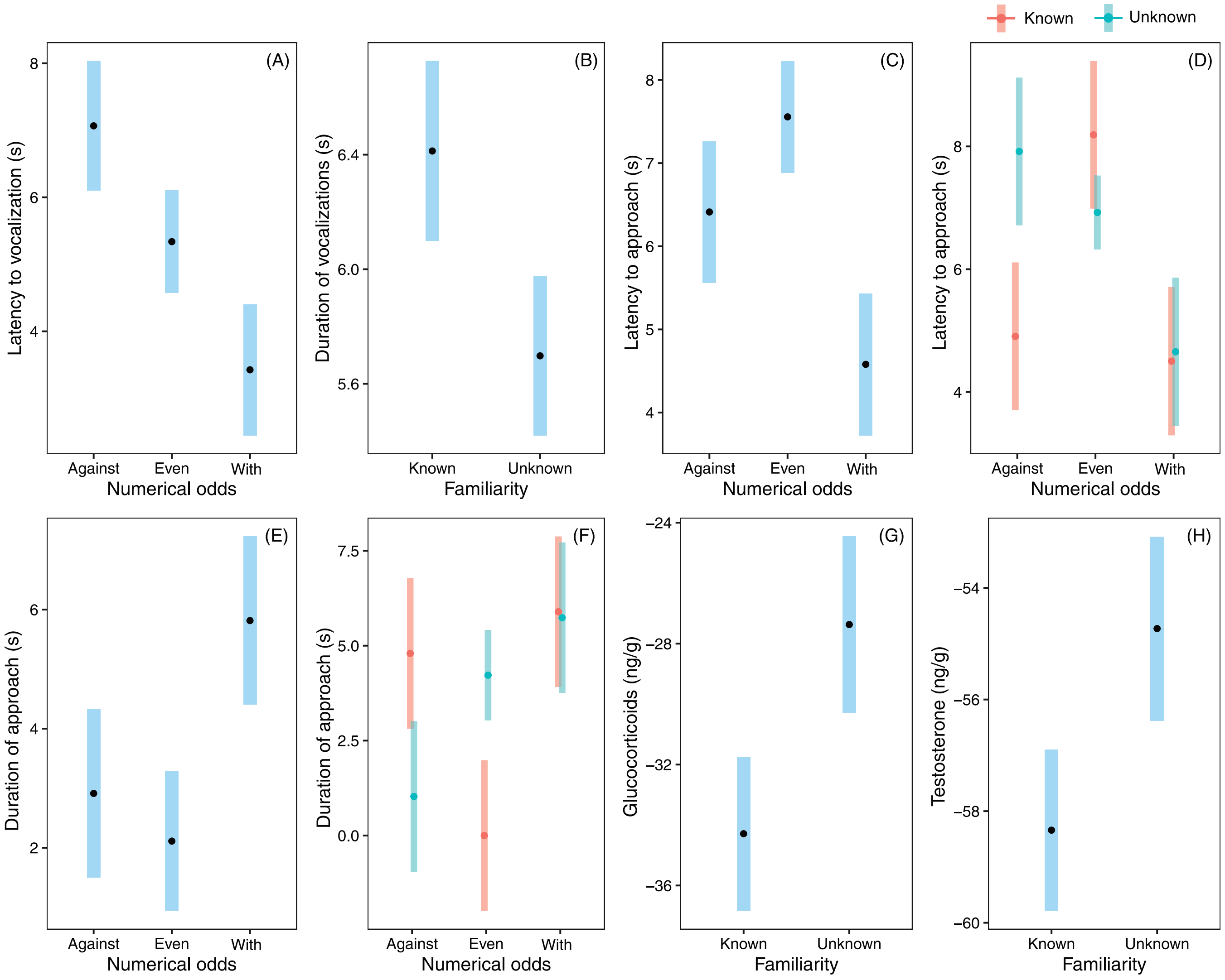

FIGURE 1 | Estimated marginal means (black dots) and 95% confidence intervals (rectangles) of models on the behavioral (A–F) and hormonal (G, H) responses of mantled howler monkey males to simulated intruder loud calls.

particularly in contexts involving potential reproductive competition (McComb et al. 1994; Temeles 1994). Our study advances our understanding by clarifying the distinct roles of numerical odds and familiarity in shaping responses to intruders in *Alouatta* and other primates.

Playback experiments may oversimplify the complexities of real-world encounters by excluding visual, olfactory, and real-time social dynamics. Future research based on multimodal stimuli incorporating these additional cues could provide more comprehensive insights into male responses (Müller and Manser 2007; Radford 2005; Tibbetts and Dale 2007). Additionally, our study focused on a single population in a specific ecological context. Differences in habitat structure, resource distribution, and intergroup dynamics may affect the generalizability of these findings. Comparative studies across populations or other species, such as black howler monkeys could help refine our understanding of these dynamics (Van Belle and Scarry 2015). Finally, individual variation in factors such as dominance rank, age, and prior experience was not addressed. Incorporating these variables could reveal additional drivers of behavioral and hormonal responses during intergroup interactions (Beehner and Kitchen 2007).

In conclusion, the interplay of familiarity, numeric odds, and their respective behavioral and hormonal effects underscores the complexity of intergroup dynamics in mantled howler monkeys. Numeric odds predominantly influence immediate decisions to engage, with shorter latency to vocalize and approach under favorable conditions. Familiarity shapes vocal duration and hormonal responses, revealing both “dear enemy” and “nasty neighbor” dynamics. Stronger hormonal responses to unfamiliar intruders are consistent with the “dear enemy” effect, as unpredictability heightens perceived threat. Conversely, prolonged vocal engagement with familiar intruders aligns with the “nasty neighbor” effect, reflecting the need to manage ongoing territorial relationships. These findings suggest that numeric odds primarily drive strategic engagement in immediate contexts, while familiarity modulates longer-term behavioral and physiological adjustments. Together, these factors demonstrate the adaptive nature of male mantled howler monkey responses to intergroup encounters and provide a robust framework for future research into conflict and cooperation across taxa.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.