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Learning to fear: predator recognition in giraffes is shaped by evolved sensitivity and ecological experience

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Introduction: Predator recognition is essential for prey survival, yet, whether responses are shaped by evolutionary predispositions or by ecological experience remains debated.

Methods: We tested vigilance responses of fifty-one free-ranging Southern giraffes (*Giraffa giraffa*) to controlled playbacks of lion roar-grunt sequences in two South African populations: a predator-naïve population in a reserve without lions and a predator-experienced population in a reserve where lions were reintroduced five years ago.

Results: Both populations oriented rapidly to lion calls, suggesting that acoustic features of lion vocalizations act as generalized danger cues. However, predator-experienced giraffes sustained vigilance ten times longer (mean $\pm$ SD: 513.34 $\pm$ 421.34 s, N = 24) compared to predator-naïve giraffes (49.06 $\pm$ 46.26 s, N = 27). Vigilance responses during lion playbacks, in general, were higher in the predator-experienced population, whereas responses to control calls did not differ between sites.

Discussion: These findings indicate that while immediate orientation likely reflects evolved sensitivity to acoustically harsh predator cues, the persistence of vigilance is shaped by ecological experience. Our study demonstrates that predator reintroduction can rapidly recalibrate prey risk perception, highlighting the dynamic interplay between evolved predispositions and learning in shaping antipredator responses.

KEYWORDS

giraffe, lion, predator-prey dynamics, behavioral ecology, landscape of fear, bioacoustics, playback, vigilance

1 Introduction

Predation is a fundamental ecological force that shapes the behavior, physiology, and cognition of prey species (Lima and Dill, 1990; Brown and Chivers, 2005). For large herbivores, the ability to detect predators early is essential for survival and shapes many behavioral trade-offs, including the balance between time spent foraging and vigilance

(Beauchamp, 2015). Across African savannas, resource gradients and predation risk jointly shape the spatial distribution, habitat use, and associations of herbivores. In particular, lions (*Panthera leo*) influence herbivore habitat selection and temporal activity patterns through both long-term and short-term predation risk (Valeix et al., 2009a, 2009; Creel et al., 2014; Anderson et al., 2016). Such spatial overlap among prey species, and shared exposure to common predators, creates opportunities for interspecific information transfer and the evolution of generalized responses to threat cues (Magrath et al., 2015; Goodale et al., 2020).

Prey species rely on different sensory cues to assess predation risk. When visual information is constrained by distance, habitat structure, or time of day, acoustic cues often become particularly important (Templeton et al., 2005; Hettner et al., 2014). These cues include both direct predator vocalizations and heterospecific alarm calls. While predator calls may provide reliable information on the type and proximity of a threat, heterospecific alarms can expand the information available to prey by effectively increasing the number of individuals scanning for danger (Magrath et al., 2015, 2020). Large African ungulates, for instance, are known to eavesdrop on alarm calls of other species, with response strength varying according to the reliability of the caller as an indicator of shared predators (Palmer and Gross, 2018). Responses to such calls may bring immediate benefits, such as increased vigilance or rapid escape, but can also have longer-term advantages, including enhanced foraging opportunities and the associative learning of predator identities (Magrath et al., 2015). The effectiveness of these cues often depends on their structural features, such as harshness, chaotic elements, or non-tonality, which can signal urgency or arousal (Morton, 1977; Briefer, 2012). Such findings illustrate that ungulates discriminate acoustic cues based on their ecological relevance, a prerequisite for adaptive predator recognition across sensory modalities.

A central question in this context is whether predator recognition is innate or shaped by learning, or both. Threat sensitivity emerges through experience, allowing individuals to fine-tune their responses to ecologically relevant dangers. For instance, harbor seals (*Phoca vitulina*) respond strongly to unfamiliar fish-eating killer whale (*Orcinus orca*) calls but ignore calls from local, non-threatening killer whales (Deecke et al., 2002). Rodents acquire recognition of raptor calls through associative learning (Kindermann et al., 2009), and burrowing bettongs (*Bettongia lesueur*) develop visual predator recognition only after repeated exposure (Steindler et al., 2020). These findings suggest that learned predator recognition allows animals to calibrate their responses to local threat conditions, helping to avoid unnecessary responses while maintaining appropriate vigilance. In ungulates, exposure to lions enhances responsiveness to lion roars (Makin et al., 2019), and primates are more likely to recognize predator cues when threats are ecologically relevant (Sánchez-Vidal et al., 2024). These findings support the idea that predator recognition in long-lived species involves both evolved predispositions and learned components. Moreover, studies show that predator-naïve populations may lose or attenuate antipredator responses over time, as demonstrated by Vancouver Island marmots (*Marmota vanancouverensis*) that lost predator discrimination in captivity after

just a few generations (Dixon-MacCallum et al., 2021). In contrast, other species retain antipredator responses for millennia, such as California ground squirrels (*Spermophilus beecheyi*), which maintain rattlesnake recognition even after more than 70,000 years of isolation (Blumstein, 2006). Such variation highlights how ecological context and evolutionary history interact to determine whether antipredator responses degrade or persist. These dynamics can be further understood within a landscape-of-fear framework, where spatial and temporal variation in risk modulates the trade-offs between foraging and vigilance (Creel et al., 2014; Laundré et al., 2014). Understanding how these processes operate in large herbivores is particularly important, as many ungulates now persist in landscapes where predator distributions are changing through recolonization and reintroduction (Hunter et al., 2007; Hayward and Somers, 2009; Chapron et al., 2014).

Recent studies further demonstrate that the return of large carnivores, such as lions, can reshape prey demography, habitat use, and risk perception (Annear et al., 2023). These questions are particularly relevant for ungulates, which provide valuable systems for examining how predator recognition interacts with ecological experience. Among them, giraffes (*Giraffa* spp.) represent an ideal model species. Although often assumed to rely primarily on visual cues due to their height and visual range (Coimbra et al., 2013; Williams, 2016), giraffes remain vulnerable to lion predation, with both calves and adults targeted (Hayward and Kerley, 2005). Their vigilance behavior is influenced by social context (Cameron and du Toit, 2005; Marealle et al., 2020), but their use of acoustic cues for predator detection remains largely unexplored. A recent study, however, demonstrated that giraffes responded more strongly to heterospecific alarm calls from red-billed oxpeckers (*Buphagus erythrorhynchus*) by sustaining vigilance for longer durations in lion-inhabited areas compared to areas without lions, with responses modulated by the acoustic harshness of the calls (Baotic and Szipl, 2025). These findings indicate that giraffes incorporate heterospecific acoustic cues into their risk assessment and that prior predator exposure enhances responsiveness to alarm calls. The study also showed that oxpecker alarm calls are acoustically harsh, suggesting that call structure interacts with ecological experience to shape vigilance behavior. This raises the question of whether such experience-dependent modulation extends to direct predator cues, such as lion roars, which are the focus of the present study.

Because acoustic cues convey information not only through context but also through their structural properties, understanding the acoustic features that underlie such responses is critical. Nonlinear phenomena (including subharmonics, biphonation, and deterministic chaos) in animal vocalizations are commonly associated with heightened arousal and are frequently observed in alarm signals across taxa (Wilden et al., 1998). A recent review highlights that nonlinear phenomena (NLP) are widespread in vertebrate vocal repertoires and are thought to have evolved to enhance signal salience, attract attention, prevent habituation, and convey arousal, threat, or distress through perceptual harshness (Massenet et al., 2025). One way to quantify this harshness is through the 'harmonic-to-noise ratio' (HNR), which measures the relative contribution of harmonic versus noisy components in a

signal. Lower HNR values often result from the presence of NLP and indicate reduced harmonic structure and increased noisiness, thereby producing acoustically harsher sounds that are more attention-grabbing (Riede et al., 2005). However, detectability alone does not determine behavioral responses; cue interpretation is modulated by prior experience and ecological context (Blumstein, 2006; Fardell et al., 2020). These dynamics are consistent with theoretical frameworks that describe antipredator behavior as a function of both evolved sensitivity to threat-related cues and individual learning history (Sih et al., 2010). Such processes are especially pronounced in ecosystems undergoing predator restoration, where the return of large carnivores like lions alters prey experience, learning opportunities, and risk perception (Hunter et al., 2007; Hayward and Somers, 2009; Palmer et al., 2022; Annear et al., 2023).

To examine how acoustic signal structure and ecological experience shape predator recognition, we conducted a playback experiment on two free-ranging giraffe populations in South Africa: one in a lion-free reserve (naïve) and one in a reserve with recently introduced lions (experienced). Individuals were presented with lion roar-grunt playback sequences (a biologically relevant predator cue), and dove coo calls (neutral control). We quantified behavioral responses, particularly vigilance, and analyzed stimulus structure focusing on HNR to assess whether acoustic harshness influences perceived threat. Based on this framework, we formulated two non-mutually exclusive hypotheses: (1) giraffes exhibit a predisposed sensitivity to predator vocalizations even in the absence of exposure, and (2) ecological experience shapes the magnitude of antipredator responses. We predicted that if predator vocalizations are inherently salient, giraffes in both populations would show immediate orienting responses and engage in vigilance. Conversely, if ecological experience is key, predator-experienced individuals would sustain vigilance for longer durations, especially in response to acoustically harsh (low-HNR) stimuli.

This study builds on previous research on predator recognition in ungulates, which has primarily focused on whether animals detect predator cues, typically characterizing responses as present or absent (e.g. Makin et al., 2019). In contrast, we compare populations that differ in long-term exposure to predators and quantify not just detection, but the magnitude and duration of antipredator behavior. By integrating ecological context with acoustic signal structure, we provide a more nuanced understanding of how predator recognition can persist, degrade, or intensify depending on risk exposure. Through the integration of acoustic, ecological, and behavioral perspectives, our study offers new insight into the mechanisms underlying antipredator plasticity and predator recognition in giraffes.

2 Material and methods

2.1 Study sites and subjects

This study was conducted between July and September 2024 at two private reserves in South Africa's Limpopo Province, chosen to

represent contrasting predator exposure histories in wild Southern giraffes (*Giraffa giraffa*). Lapalala Wilderness (LW; 48,000 ha) inhabits a resident lion population introduced between 2019 and 2020, which had grown to 15 individuals by the time of this study. In contrast, Mogalakwena River Reserve (MRR; 1,500 ha) remains free of large predators and thus provides a predator-naïve comparison group. Both study sites represent comparable dry-season savanna habitats, with similar vegetation structure and visibility, minimizing potential confounds related to habitat differences. To localize and approach giraffes for testing, site-specific methods were employed. At MRR, individuals were followed on foot by a single habituated observer (AB), using slow and non-invasive approaches to prevent disturbance. Giraffes at this site were well accustomed to human presence due to a long-term behavioral monitoring project conducted prior to this study. At LW, giraffes were located using a DJI Mini 4 Pro drone flown at altitudes between 40 and 70 meters, after which they were approached by vehicle. Giraffes at LW were habituated to vehicle presence through regular exposure to park management and monitoring activities and have shown no disturbance-related behaviors in previous playback experiments (Baotic and Szipl, 2025). Drone use was limited to pre-trial localization and never coincided with playback experiments or behavioral recording. In both reserves, giraffes were only tested once they were stationary, feeding calmly, and showed no signs of alertness, ensuring that vigilance responses reflected stimulus perception rather than observer disturbance. Evidence of active predation pressure at LW is supported by giraffe carcasses with confirmed signs of lion predation (Annear et al., 2023). Importantly, MRR is not bordered by reserves or farms containing lions, ensuring that giraffes at this site had no opportunity for exposure to lion vocalizations or predation risk. We focused exclusively on adult giraffes of both sexes. Individuals were identified based on their unique coat patterns (Shorrocks and Croft, 2009; Miele et al., 2021) and classified as adults following morphological and developmental criteria established by Muller (2018). A total of 27 individuals were included at MRR (13 females, 14 males) and 24 at LW (12 females, 12 males).

2.2 Acoustic stimuli

We used two categories of auditory stimuli in playback trials: lion roar-grunt calls (Figure 1A), and ring-necked dove (*Streptopelia capicola*) coo calls (Figure 1B). Lion vocalizations served as biologically relevant predator cues (Grinnell and McComb, 2001), while dove calls acted as a non-threatening control (Slabbekoorn et al., 1999). Dove calls were selected due to their function as neutral conspecific contact signals and absence of alarm-related associations in the literature. Playback stimuli were compiled into standardized packages, each containing two playback sequences. Within each sequence, lion or dove calls were presented as temporally naturalistic bouts, with inter-call intervals matched across packages. Dove calls were sourced from a previous playback experiment conducted by the authors of this study (Baotic and Szipl, 2025). Lion calls were sourced from existing archives and

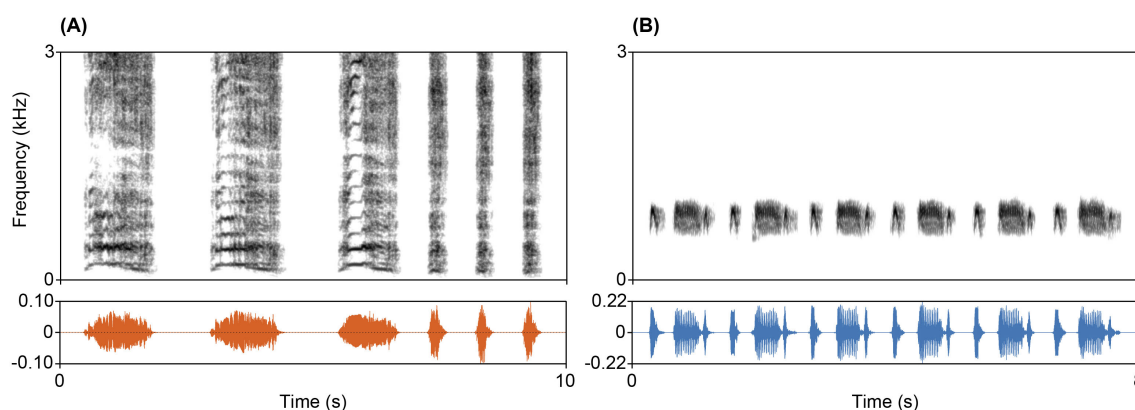


FIGURE 1
Spectrograms and oscillograms of acoustic stimuli used in the playback experiment. **(A)** Lion (*Panthera leo*) vocalization sequence (recorded by Timmy Moser), consisting of three full roars followed by three grunts. The mean harmonic-to-noise ratio (HNR) of this stimulus was 5.3 dB. **(B)** Ring-necked dove (*Streptopelia capicola*) stimulus composed of six coo calls with a mean HNR of 19.6 dB. Spectrograms were generated in Praat using a fast Fourier transform (FFT) method with a dynamic range of 55.0 dB. Window length was set to 0.08 s for the lion stimulus and 0.03 s for the dove stimulus.

collaborators (see acknowledgements), ensuring a diverse representation of male and female vocalizations. Lion recordings were visually inspected for signal clarity and absence of audio artifacts (no overlap with other audio signal or friction sounds) by using spectrograms in Audacity version 3.3 (Audacity Team, 2023). Only sequences with an intact acoustic structure and no interfering background signals were retained. To minimize ambient noise in the playback signals, we applied the ‘noise reduction’ effect in Audacity. Noise profile filtering has been shown to effectively reduce background noise while preserving the acoustic properties of vocalizations (Baker and Logue, 2007; Benedict et al., 2021). A one-second noise profile was created before the onset of a call, followed by a 4–10 dB noise reduction (depending on the recording’s acoustic characteristics), using a sensitivity setting of 6.0 and three frequency smoothing bands. To further enhance sound clarity, additional spectral content filtering was performed in Praat version 6.4.27 (Boersma and Weenink, 2025). A high-pass filter was applied to remove excess low-frequency background noise below 450 Hz for dove calls, and below 30 Hz for lion calls. A low-pass filter was used to remove upper ambient frequencies, cutting off above 1.3 kHz in dove calls and above 20 kHz in lion calls. To ensure consistent peak amplitude across all sequences, while avoiding distortion due to excessive loudness (clipping effect), we normalized the audio files to -1.0 dB peak amplitude using Audacity. To ensure consistent stimuli conditions, the sound pressure level (SPL) of each playback sequence was standardized to 85 dB (Z-weighted) using an NTI AL1 SPL meter with an NTI MiniSPL microphone.

Lion and dove single calls served as templates to create 27 playback packages, each containing two sequences - one for each species. Lion sequences contained three ‘roar’ and three ‘grunt’ calls, and dove sequences contained six ‘coo’ calls. A total of 84 lion roars (1.6 ± 0.3 s) and 84 lion grunts (0.6 ± 0.2 s) from fifteen individuals and 126 dove perch-coo calls (1.1 ± 0.05 s) were used, with values given as mean $\pm$ standard deviation (SD). The calls per sequence, as

well as the order of sequences within each package, were randomly assigned to control for order effects.

2.3 Playback experiment procedure

Propagation tests, using a JBL-EON Compact loudspeaker (37.5 Hz to 20 kHz frequency response) connected via Bluetooth to an Apple iPhone 14 Pro, confirmed that spectral properties of playback stimuli remained intact at distances up to 150 meters. Lion and dove stimuli were re-recorded using a Sound Devices MixPre-3 II (frequency response: 10 Hz to 80 kHz) and an omnidirectional Neumann KM 183 MT microphone, saved as *.wav files (44.1 kHz, 16-bit). Spectrograms of lion vocalizations are provided in Supplementary Figure S1 and for dove calls in Supplementary Figure S2 in the Supplementary File 1.

Vigilance behavior was recorded as the primary response variable. Given the established role of risk assessment and predator detection in African ungulates (Creel et al., 2014), we identified vigilance behavior as the primary response variable. Both predation risk and social factors shape vigilance in giraffes (Cameron and du Toit, 2005). To isolate responses to predator cues and avoid conspecific influences, only one giraffe at a time was tested, with no other individuals nearby. This ensured that vigilance was attributable solely to lion calls, controlling for collective vigilance effects.

Playback trials were conducted between 09:30 and 17:40, i.e. after sunrise and before sunset, to avoid the crepuscular periods when lions are typically most active and to ensure consistent daylight conditions. Trials were carried out under calm weather conditions to prevent scattering of the sound stimuli due to wind gusts. At MRR, giraffes were followed on foot during their feeding activities and approached slowly to prevent premature disturbance, allowing them to habituate to the observer (Anton Baotic). Due to LW’s vast size, we used a DJI Mini 4 Pro drone to localize giraffes.

Once located, the giraffes were followed by vehicle prior to trial initiation.

Individual giraffes were observed until they displayed relaxed feeding behavior, defined as continuous browsing with no visible signs of alertness. Trials were initiated only when the focal animal was stationary and no other conspecifics were within the visible vicinity, minimizing the influence of social facilitation or group vigilance. To ensure that the measured behavior reflected responses to playback stimuli alone, we confirmed that no vehicles from reserve staff were present in the area.

The JBL-EON Compact speaker was hidden behind vegetation to prevent stimulus association with the observer and speaker, respectively, and positioned to face the giraffe. Once the animal had engaged in uninterrupted feeding for a minimum of 10 seconds, we initiated the playback sequence (lion or dove). Each sequence followed a three-phase structure: (1) baseline (pre-stimulus behavior), (2) response (during stimulus), and (3) post-response (resumption of feeding for 10 seconds after playback). When individuals moved after the first sequence (i.e., before fully completing the experiment), the observer followed and resumed trials once the animal returned to calm foraging. Each of the 51 individuals included in the dataset was tested twice, once with a lion playback and once with a dove playback, within the same day, ensuring no day-to-day variation within individuals. We further documented the distance between the speaker and the giraffe using a Nikon Prostaff 1000 laser rangefinder (range: 20–133 meter). The experimental setup is illustrated in Figure 2.

2.4 Behavioral data collection and coding

Behavioral responses were recorded using a Sony FDR-AX53 video camera. Videos were later coded frame-by-frame (20 ms resolution) using Solomon Coder 17.03 for Windows. We used continuous sampling and recorded the duration (in seconds) of predefined behavioral categories including ‘Feeding’ (mouth attached to foliage and feeding continuously for ≥ 10 s), ‘Not feeding’ (cessation of feeding), ‘Turn to’ (orienting toward the sound source), ‘Scanning’ (stationary vigilant posture with head/

neck raised, screening/monitoring environment), ‘Approach-Investigation’ (cautious movement toward the sound source), ‘Displacement’ (walking continuously in the opposite direction of the loudspeaker for ≥ 10 s), and five ear postures indicative of attentional state (illustrated in Figure 3). We note that ‘Approach-Investigation’ is considered a vigilance response in giraffes, reflecting cautious investigative movements toward a novel or potentially threatening stimulus rather than attraction (Langman, 1977). Behavioral definitions followed an ethogram previously established and validated in (Baotic and Szipl, 2025), with full behavioral definitions provided in Table 1. If the focal giraffe exhibited displacement behavior, the playback trial was considered complete. If the focal giraffe showed displacement behavior by walking continuously in the opposite direction of the loudspeaker for at least 10 seconds, the playback trial was considered complete.

In addition to behavioral durations, we measured latencies to ‘Not feeding’ and to orient toward the speaker (‘Turn to’ and ‘Scanning’). If a behavior did not occur within 20 seconds of stimulus onset, the maximum value of 20 seconds was assigned by the coding software. These censored values indicate the absence of a measurable response and were excluded from the calculation of mean latencies.

Inter-rater reliability was not reassessed in the current study, as all behavioral categories and coding procedures followed the validated protocol established by Baotic and Szipl (2025).

2.5 Acoustic characterization of stimuli

To quantify the acoustic structure of the playback stimuli, we analyzed both call durations and signal tonality using Praat (version 6.4.27). For each playback package, we calculated the average harmonic-to-noise ratio (HNR) across all included calls, providing a proxy for the relative contribution of harmonic versus noisy components in the signal (Boersma and Weenink, 2025). HNR has previously been shown to correlate with perceptual judgments of roughness and vocal harshness in non-human animal vocalizations (Riede et al., 2005), making it a relevant measure for evaluating

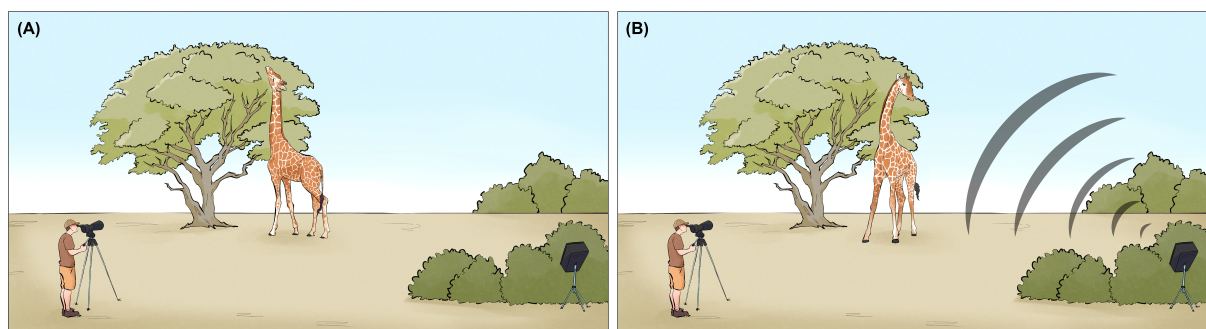
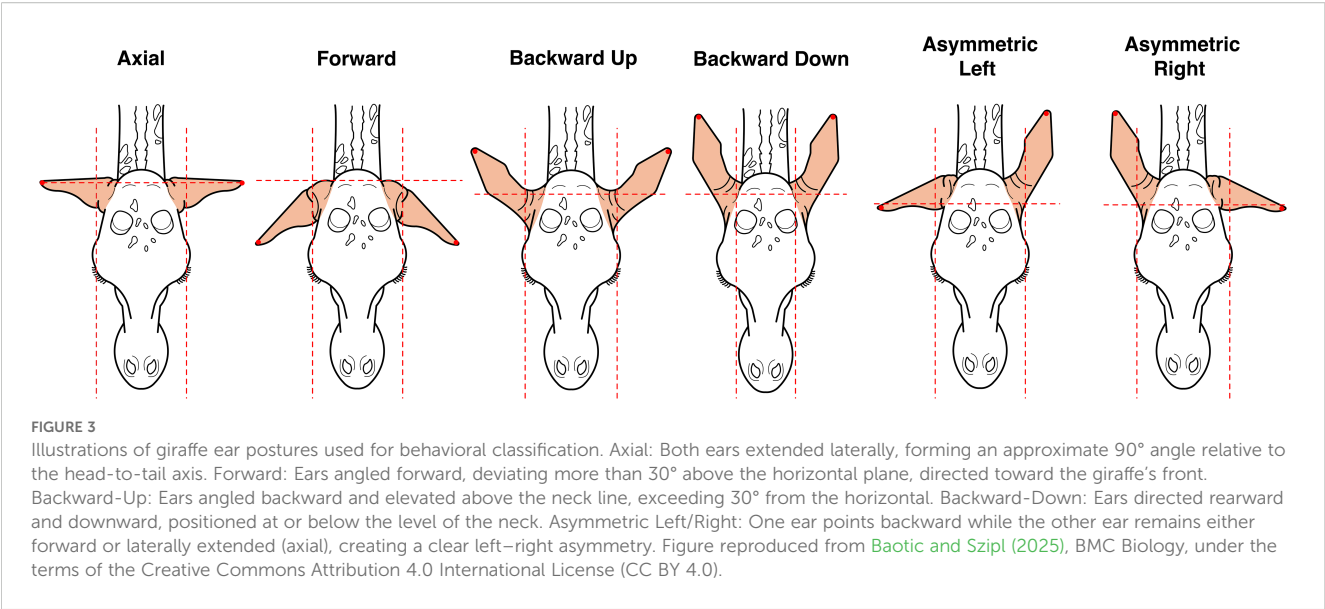


FIGURE 2

Experimental setup of a playback. (A) The focal giraffe feeds stationary at a tree, (B) and turns toward the hidden speaker responding to a lion roar-grunt sequence. Figure reproduced from Baotic and Szipl (2025), BMC Biology, under the terms of the Creative Commons Attribution 4.0 International License (CC BY).



acoustic salience. HNR values were derived using the ‘To Harmonicity (cc)’ function with the following settings: a time step of 0.001, a silence threshold of 0.1, and one period per window. We adjusted the minimum pitch floor to match species-specific vocal properties, 450 Hz for dove calls and 30 Hz for lion calls. Call durations were obtained using the ‘Get total duration’ command. The resulting mean HNR values served as a continuous acoustic predictor variable in our statistical analyses, enabling us to examine whether variation in signal structure influenced behavioral responses.

TABLE 1 Definitions of the behaviors used to analyze giraffes’ responses to playback stimuli.

Behavior	Definition
Feeding	The individual engages in continuous consumption of leaves or branches with observable mouth-to-vegetation contact for at least 10 seconds.
Not feeding	The individual halts feeding behavior entirely, showing no further interaction with foliage.
Turn to	The individual stops feeding and directs its head and neck toward the speaker or sound source. This initial orientation response is recorded only once.
Ear posture	The five ear positions (‘Axial,’ ‘Forward,’ ‘Backward up,’ ‘Backward down,’ ‘Asymmetric left/right’) are used to assess attentional states.
Scanning	Following the ‘Turn to’ response, the individual actively moves its head to observe the surroundings. Revisiting the speaker’s direction is included in this behavioral category.
Approach-Investigation	Focal giraffe cautiously moves toward the sound source, either in a straight line or in arcs/semi-circles, while maintaining vigilance. The behavior requires at least three steps in the direction of the loudspeaker. Approaches may terminate in a pause with an attentive posture directed toward the loudspeaker, in which case ‘Scanning’ is coded.
Displacement	The individual walks continuously for at least 10 seconds in the opposite direction of the loudspeaker.

2.6 Statistical analysis

We conducted a principal component analysis (PCA) to reduce the number of behavioral responses coded from the video recordings of the response phases into a smaller set of components. The PCA yielded one main principal component (PC; eigenvalue >1.0) that explained 92.6% of the total variance. This component reflected the duration of vigilance-related behaviors, with higher scores indicating longer vigilance responses. The PC was driven by the durations of ‘Not feeding,’ ‘Ears forward,’ ‘Ears asymmetric,’ ‘Vigilance’ (this variable comprised not feeding, turning toward the sound source, approach-investigation and scanning), and ‘Total response time,’ with only ‘Ears forward’ and ‘Ears asymmetric’ among the ear postures contributing meaningfully (Table 2). This PC captured both initial reactions to stimuli (not feeding and turning toward the sound source, ears forward) and sustained alert behaviors (scanning, approach-investigation, total response duration). Therefore, we termed this component the ‘vigilance behavior’ component. Behavioral categories with eigenvalues below 1.0 that loaded onto separate PCs were discarded. The overall Kaiser-Meyer-Olkin measure of sampling adequacy (MSA) was 0.82, with estimates ranging from 0.77 to 0.94, confirming the data was suitable for PCA. We extracted regression scores of the PC for further analyses. All behavioral categories had positive loadings on the PC (cp. Table 2). Thus, higher positive regression scores translate to higher values of the behavioral categories summarized in this PC, and can be interpreted as longer durations of vigilance behaviors.

We applied Linear Mixed Models (LMMs) with a Gaussian distribution and an identity link function to assess the effects of the different stimuli and various individuals and environmental factors on the ‘vigilance behavior’ component. We first assessed multicollinearity between fixed effects (Zuur et al., 2009) and detected high collinearity between stimulus type and mean HNR

TABLE 2 Behavioral responses to playbacks (in seconds) were summarized using principal component analysis (PCA) with ‘varimax’ rotation.

Behavioral categories	Behavioral response duration (s), mean ± standard deviation	PCA			
		PC	h ²	u ²	MSA
Total response time	141.1 ± 295.0	0.998	0.996	0.004	0.77
Total vigilance	133.8 ± 293.5	0.998	0.996	0.004	0.79
Ears forward	114.1 ± 246.7	0.981	0.963	0.037	0.82
Not feeding	119.9 ± 269.8	0.974	0.949	0.051	0.94
Ears asymmetric	15.6 ± 39.9	0.851	0.724	0.276	0.82

Standardized loadings (PC), communalities (h², the variance explained by the item), uniqueness (u²), and the Kaiser-Meyer-Olkin measure of sampling adequacy (MSA) for each item are shown. Overall MSA = 0.82. Sample sizes: Mogalakwena River Reserve (MRR, predator-naïve population): 27 individuals (13 females, 14 males); Lapalala Wilderness (LW, predator-experienced population): 24 individuals (12 females, 12 males).

of the stimuli. Thus, we run two separate LMMs, fitted by maximum likelihood, either including stimulus type or mean HNR as a fixed effect. The identity of each test individual (giraffe ID) was included as a random effect to account for repeated measures of the same individuals when testing different stimuli. The first LMM examined the effects of stimulus type and reserve on the ‘vigilance behavior’ component, with giraffe ID as a random intercept. The full model included stimulus type, reserve, sex, playback order, and the interaction of stimulus type and reserve. The second LMM investigated the effects of acoustic-related features of the stimuli on the ‘vigilance behavior’ component. The full model contained the fixed effects HNR, reserve, sex, stimulus order, and the HNR × reserve interaction. Likelihood Ratio Tests (LRT) were used to compare the null models containing only the random effect and the intercept with full models (either containing stimulus type or mean HNR).

To ensure that vigilance responses were not affected by potential confounding variables, we tested for the effects of both playback distance and time of day. An additional LMM including distance (in meters) as a covariate and its interaction with reserve, while retaining the stimulus type × reserve interaction and giraffe ID as a random effect, confirmed that vigilance responses were not confounded by variation in playback distance (see [Supplementary Table S4](#) in [Supplementary File 1](#)). Likewise, a Spearman rank correlation between vigilance component scores and time of day, calculated for lion trials only, revealed no significant relationship ($\rho = -0.19$, $N = 51$, $p = 0.17$). Time of day for each playback was extracted from the video time stamps and converted to decimal hours (e.g., 14:32 = 14.53 h) using the formula hour + minute/60 + second/3600 in Excel. As neither distance nor time of day influenced vigilance behavior, these factors were not included as covariates in the final models.

To investigate whether response speed to lion playbacks differed between lion-experienced and lion-naïve giraffes, we analyzed the latencies of vigilance-related behaviors following lion roar-grunt sequences. Because latency values were only available for trials in which a behavioral response occurred within 20s of playback onset, trials without a detectable response were excluded from the latency dataset. We selected the behavioral responses ‘Not feeding’, ‘Scanning’, and ‘Turn to’, which represent immediate vigilance responses and also contributed to the vigilance behavior

component derived from the PCA. As sample sizes varied among behaviors and were in some cases too small to reliably fit mixed models, we used non-parametric pair-wise Mann-Whitney U tests to compare latencies between reserves.

Statistical analyses were conducted in R Studio Version 2024.12.1 + 563 ([RStudio Team, 2025](#)), with R Version 4.4.3 ([R Core Team, 2025](#)), with following packages: ‘psych’ ([Revelle, 2024](#)) for PCA, ‘lme4’ ([Bates et al., 2015](#)) for LMMs, ‘emmeans’ ([Lenth, 2025](#)) to conduct pairwise comparisons of interaction terms (*post hoc* tests, with Tukey-adjusted *p* values). The dataset generated and analyzed during this study is included in this article and its [Supplementary File 2](#).

3 Results

3.1 Behavioral responses to stimulus type

To examine how giraffes respond to predator cues, we fitted a LMM to PC scores representing the ‘vigilance behavior’ component, with descriptive statistics of the underlying behavioral measures provided in [Supplementary Table S1](#). The model included fixed effects for stimulus type (lion vs. dove), reserve (LW vs. MRR), sex, playback order, and the interaction between stimulus type and reserve. The model significantly outperformed the null model containing only the random intercept (Likelihood ratio test: $\chi^2(5) = 78.513$, $p < 0.0001$).

There was a strong interaction between stimulus type and reserve ($\beta = -1.578$, $SE = 0.268$, $t = -5.892$, 95% CI = $[-2.111, -1.046]$), indicating that the effect of lion versus dove stimuli on vigilance behavior differed markedly between sites. Overall, giraffes showed stronger vigilance responses to lion than to dove calls ($\beta = 1.745$, $SE = 0.195$, $t = 8.965$, 95% CI = $[1.358, 2.131]$), an effect that was strongest among predator-experienced individuals. No meaningful effects were found for sex, order, or reserve alone. For a tabular overview of all coefficients, see [Table 3](#).

Pairwise comparisons of estimated marginal means (Tukey-adjusted) confirmed that vigilance responses to lion calls were significantly stronger at the predator-experienced reserve (LW) than at the predator-naïve site (MRR; $\beta = 1.585$, $SE = 0.196$, $t = 8.088$, $p < 0.0001$), whereas responses to dove calls did not

TABLE 3 Effect of stimulus type on 'vigilance behavior' component.

Coefficients	EM	SE	t value	CI lower	CI upper
(Intercept)	-0.471	0.168	-2.805	-0.802	-0.139
Stimulus type (Dove vs. Lion)	1.745	0.195	8.965	1.358	2.131
Reserve (LW vs. MRR)	-0.007	0.190	-0.036	-0.383	0.369
Sex (female vs. male)	-0.131	0.135	-0.972	-0.400	0.138
Playback order (1st vs. 2nd)	0.173	0.134	1.290	-0.093	0.439
Stimulus Type: Reserve	-1.578	0.268	-5.892	-2.111	-1.046

Estimated means (EM), standard errors (SE), effect sizes (t-values), and 95% lower and upper confidence intervals (CI) for all coefficients in the LMM examining the effect of stimulus type. The model includes stimulus type (lion vs. dove), reserve (LW vs. MRR), sex, and playback order on the regression scores of the vigilance behavior component, as well as the interaction between stimulus type and reserve. Strong effects (CI not overlapping zero) of stimulus type and the stimulus type $\times$ reserve interaction are indicated in bold. No strong main effects were found for sex, reserve, or playback order. The colon indicates the interaction between stimulus type and reserve. Sample sizes: Mogalakwena River Reserve (MRR, predator-naïve population): 27 individuals (13 females, 14 males); Lapalala Wilderness (LW, predator-experienced population): 24 individuals (12 females, 12 males).

differ between reserves (Table 4). As shown in Figure 4A, vigilance-related PC scores were clearly elevated during lion trials at LW, while individuals at MRR (predator-naïve) showed little differentiation between the two stimuli.

Representative video samples from both study sites demonstrate the differential responses at MRR, a predator-naïve male giraffe briefly orients toward the lion roar-grunt playback and shows no response to the dove coo call (Video S1), whereas at LW, a predator-experienced male giraffe sustains vigilance for a longer duration when exposed to the lion stimulus, also showing no response to the dove stimulus (Video S2; see also Supplementary File 1 for DOIs).

3.2 Influence of harmonic-to-noise ratio and ecological context

The second LMM assessed whether acoustic features of the stimuli, particularly the harmonic-to-noise ratio (HNR), influenced giraffe vigilance behavior, as represented by PC regression scores. The full model included HNR, reserve (LW vs. MRR), sex, stimulus order, and the HNR $\times$ reserve interaction as fixed effects, with giraffe ID as a random factor. Compared to the null model, the full

model explained significantly more variation in vigilance behavior (LRT: $\chi^2(5) = 65.818$, $p < 0.0001$).

Analysis of fixed effects showed a pronounced negative main effect of HNR ($\beta = -0.117$, $SE = 0.015$, $t = -7.649$, $CI = [-0.15, -0.09]$), indicating that giraffes showed stronger vigilance responses to acoustically harsher stimuli. In our dataset, lion roar-grunt sequences had substantially lower HNR values ($HNR = 6.6 \pm 2.0$) than dove coo calls ($HNR = 19.3 \pm 2.3$), confirming that low HNR was associated with the predator stimulus. Giraffes at LW also exhibited greater vigilance compared to those at MRR ($\beta = -2.165$, $SE = 0.313$, $t = -6.926$, $CI = [-2.78, -1.55]$). Crucially, there was an interaction between HNR and reserve ($\beta = -1.105$, $SE = 0.021$, $t = -4.887$, $CI = [-0.06, -0.15]$) revealing that the effect of acoustic harshness varied by location (pairwise contrast: $\beta = 0.807$, $SE = 0.147$, $t = 5.478$, $p < 0.0001$). Sex and playback order had no influence on the vigilance behavior. For a tabular overview of all coefficients, see Table 5.

To further examine whether HNR effects simply reflected species identity, we tested for a relationship between HNR values of lion calls and giraffe vigilance responses (PC scores) within lion trials only ($N = 51$). This correlation was not significant (Spearman's $\rho = 0.013$, $p = 0.929$), indicating that variation in HNR among lion calls did not predict vigilance responses. Thus, the effect of HNR on response strength primarily reflects the broad contrast between lion and dove calls rather than within-species variation.

Predator-experienced giraffes were more sensitive to changes in HNR, with calls of lower HNR eliciting stronger vigilance (reflected by higher regression scores of the PC) than in predator-naïve individuals (Figure 4B). These results suggest that both call structure and ecological context potentially shape antipredator responses in giraffes. Vigilance increased most strongly to stimuli with low harmonic-to-noise ratios, which in this case were lion roars. This pattern was especially pronounced in predator-experienced individuals, highlighting a potential role of experience or habitat-associated risk in modulating acoustic threat assessment.

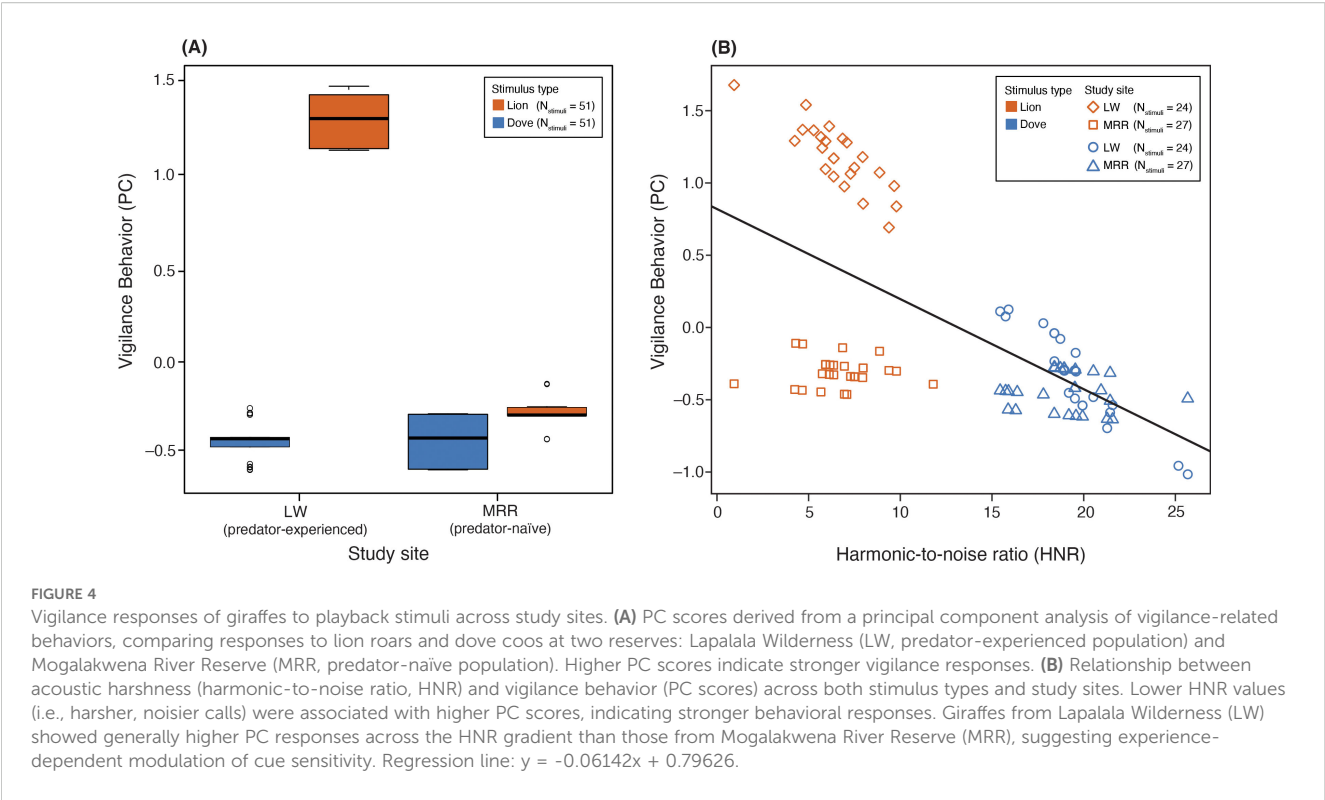
3.3 Response latencies to lion playback stimuli

Mann-Whitney U tests revealed no significant differences in response latencies between the two reserves for any of the behaviors

TABLE 4 Simple pairwise contrasts derived from the LMM for the interaction between stimulus type (Dove vs. Lion) and reserve (Lapalala Wilderness, LW vs. Mogalakwena River Reserve, MRR).

Comparison type	Factor tested	Context	Estimated mean	SE	t ratio	p
LW vs. MRR	Reserve	within Dove	0.007	0.196	0.035	0.972
LW vs. MRR	Reserve	within Lion	1.585	0.196	8.088	<0.0001
Dove vs. Lion	Stimulus	within LW	-1.745	0.201	-8.698	<0.0001
Dove vs. Lion	Stimulus	within MRR	-0.166	0.19	-0.877	0.384

The table lists the estimated marginal means for each simple contrast, specifying which factor was tested (stimulus or reserve) and which context was held constant. Results are averaged over the levels of sex and stimulus order. P values were adjusted using the Tukey method. Sample sizes: MRR = 27 individuals (13 females, 14 males); LW = 24 individuals (12 females, 12 males).



(Not feeding: $U = 234.5$, $N_{LW}=24$, $N_{MRR}=26$, $p = 0.135$; Scanning: $U = 61.0$, $N_{LW}=10$, $N_{MRR}=8$, $p = 0.068$; Turn to speaker: $U = 240.5$, $N_{LW}=24$, $N_{MRR}=26$, $p = 0.168$). These findings indicate that giraffes respond rapidly to predator sounds regardless of recent exposure to predators. This supports the idea that initial sensitivity to lion calls may be partly instinctive, although experience likely shapes the strength and duration of subsequent responses. For a tabular overview of the latency measures, see [Supplementary Table S2](#) for LW and [Supplementary Table S3](#) for MRR in the [Supplementary File 1](#).

TABLE 5 Effect of mean harmonic-to-noise ratio (HNR) on giraffe vigilance behavior.

Coefficients	EM	SE	t value	CI lower	CI upper
(Intercept)	1.980	0.252	7.870	1.482	2.478
HNR	-0.117	0.015	-7.649	-0.147	-0.086
Reserve (LW vs. MRR)	-2.165	0.313	-6.926	-2.784	-1.547
Sex (female vs. male)	-0.193	0.143	-1.349	-0.477	0.090
Playback order (1st vs. 2nd)	0.127	0.143	0.887	-0.156	0.410
HNR: Reserve	0.105	0.021	4.887	0.062	0.147

Estimated means (EM), standard errors (SE), effect sizes (t-values), and 95% lower and upper confidence intervals (CI) for all coefficients in the full LMMs. The model examined the impact of mean HNR, research area, sex, and stimulus presentation order on the regression scores of the vigilance behavior component. Bold type indicates coefficients with strong effects and CI not overlapping zero. The colon indicates the interaction between HNR and reserve. Sample sizes: Mogalakwena River Reserve (MRR, predator-naïve population): 27 individuals (13 females, 14 males); Lapalala Wilderness (LW, predator-experienced population): 24 individuals (12 females, 12 males).

4 Discussion

Our study demonstrates that ecological experience strongly shapes how giraffes respond to predator vocalizations. Giraffes in a reserve where lions were reintroduced five years ago exhibited stronger and more persistent vigilance responses to lion roars than individuals from a predator-free reserve. While both populations oriented toward the lion calls, only predator-experienced giraffes maintained elevated vigilance, indicating that experience drives sustained antipredator responses. Importantly, the main effect of reserve was negligible, showing that the difference was not due to general reactivity between sites but was specifically driven by stronger responses to lion calls at the predator-experienced site. This is consistent with findings across other African ungulates, where impala (*Aepyceros melampus*) and wildebeest (*Connochaetes taurinus*) showed elevated vigilance under predation pressure (Hunter and Skinner, 1998), and zebra (*Equus quagga*), tsessebe (*Damaliscus lunatus*), wildebeest, and impala exhibited proactive antipredator responses to predator activity, with the strongest effects in impala and zebra (Bennitt et al., 2024).

Beyond the role of ecological experience, our results also point to the influence of acoustic structure. Giraffes at LW were more sensitive to changes in HNR, with lower HNR calls eliciting stronger vigilance than at MRR. Acoustic structure therefore modulated vigilance: vocalizations with lower HNR (which is typical of lion roars and grunts) elicited stronger responses, particularly in predator-experienced individuals. This suggests that acoustic harshness enhances salience and influences response strength when paired with ecological relevance. Our findings thus align

with broader evidence that prey species use acoustic structure to evaluate predation risk (Hettena et al., 2014). This aligns with findings from other species: marmots respond more strongly to alarm calls with added noise (Blumstein and Récapet, 2009), and vigilance increases under uncertainty in high-risk contexts (Bell et al., 2009). Our results suggest a dual mechanism: a predisposed sensitivity to acoustically salient predator cues (as both populations responded equally fast), and an experience-based modulation of response persistence. This pattern is consistent with prior findings in a variety of taxa where predator recognition and response intensity are shaped by prior exposure (e.g. Deecke et al., 2002; Kindermann et al., 2009; Makin et al., 2019; Steindler et al., 2020; Sánchez-Vidal et al., 2024).

Giraffes across both sites oriented rapidly to the lion playback, suggesting that certain acoustic features act as generalized danger cues. Nonlinear phenomena are widespread in mammalian vocal repertoires and are often associated with perceptual harshness, heightened salience, and signals of arousal or threat (Wilden et al., 1998; Riede et al., 2005; Massenet et al., 2025). While detailed analyses of nonlinear phenomena in lion roars are scarce, lion vocalizations are characterized by low fundamental frequencies, dense formant spacing, and noisy segments that contribute to their harsh acoustic profile (Frey and Gebler, 2010). Moreover, lions preferentially roar under atmospheric conditions that enhance sound propagation, suggesting that the calls are adapted for long-distance detectability (Wijers et al., 2021). In our dataset, lion roars were also consistently associated with low HNR, further contributing to their perceptual harshness compared to control calls. Importantly, we found no evidence that variation in HNR within lion calls predicted vigilance responses. This supports the interpretation that HNR effects are not artifacts of within-species variation but instead reflect the broad acoustic contrast between lion roars (low HNR) and dove coos (high HNR). These features make lion roars particularly difficult to ignore. While our focus is on prey responses, it is worth noting that lion roars also function in intraspecific communication, especially in territorial defense and male-male competition (McComb et al., 1994; Grinnell and McComb, 2001; Grinnell, 2002), contexts in which high detectability is advantageous. Together, these features suggest that the structure of lion vocalizations acts as a generalized cue of danger in giraffes that are capable of triggering immediate vigilance responses, even in predator-naïve individuals. Such acoustic properties likely explain why giraffes across both populations responded rapidly to lion calls. However, while orientation latencies were uniformly short, vigilance duration varied substantially between populations.

Predator-experienced giraffes maintained heightened vigilance for longer. This suggests that although the onset response may reflect evolved perceptual tuning to harsh sound structures, the persistence of antipredator behavior is shaped by ecological experience. Since lions were recently introduced to LW, with confirmed giraffe predation events (Annear et al., 2023), giraffes in this reserve may have developed heightened sensitivity to lion roars through direct predator exposure. Similar decoupling of response onset and duration has been observed in other taxa. For

instance, New Holland honeyeaters (*Phylidonyris novaehollandiae*) initiate flight within milliseconds of hearing an alarm call but adjust hiding duration based on call structure and perceived urgency (McLachlan and Magrath, 2020). Likewise, yellow-bellied marmots (*Marmota flaviventris*) responded more intensely to manipulated conspecific alarm calls containing added noisy elements than to normal calls. The added nonlinear element increased attentional engagement and reduced foraging (Blumstein and Récapet, 2009), which is consistent with broader evidence that noisy features enhance salience and delay habituation (Massenet et al., 2025). Comparable plasticity is seen in large mammals: moose (*Alces alces*), rapidly reacquired predator-specific responses after recolonization by wolves (Berger et al., 2001), and predator-experienced caribou (*Rangifer tarandus caribou*) display stronger and spatially specific avoidance than naïve conspecifics, further illustrating how ecological experience shapes the persistence and intensity of antipredator responses (Derguy et al., 2025). Together, these findings, alongside our results, align with theoretical frameworks suggesting that antipredator behavior integrates evolved sensitivity to acoustic salience with experience-based risk assessment (Lima and Dill, 1990; Stankowich and Blumstein, 2005; Fardell et al., 2020). Our results in giraffes provide a complementary example of this interplay, showing how immediate orientation to harsh acoustic cues is likely underpinned by evolved perceptual tuning, whereas the persistence of vigilance depends on ecological experience. Such behavioral plasticity is particularly relevant in rewilding contexts, where antipredator responses can degrade in predator-free environments and require reacquisition after predator return (Blumstein, 2006; Palmer et al., 2022). Comparable dynamics have recently been documented in African systems, where the reintroduction of lions has altered prey demography, vigilance, and habitat use (Annear et al., 2023). Our results also highlight how landscapes of fear are reconfigured following predator reintroduction, as prey reacquire appropriate risk responses and recalibrate vigilance behavior (Creel et al., 2014; Laundré et al., 2014).

While our study provides new insight into giraffe risk perception, several limitations warrant consideration. HNR was a useful proxy for acoustic harshness, but it does not capture all relevant features. The study also focused solely on adult individuals; including age or developmental stage could yield a more complete picture of antipredator plasticity. Although we cannot entirely exclude potential influences such as habitat structure, observer presence, or drone use, we consider these unlikely to explain the observed population-level differences. These factors were minimized through site-specific habituation protocols, pre-trial-only drone use, and structurally similar open savanna habitats across sites (see Methods for details). Potential confounding factors such as the time of day and the distance between the speaker and the focal giraffe were statistically tested and found to have no influence on vigilance responses (see Supplementary Table S4 and related analyses). This confirms that the observed population differences were not driven by experimental or contextual variation.

Future studies should examine additional acoustic parameters, such as specific nonlinear components or frequency modulation. Longitudinal or repeated-exposure studies could reveal how predator recognition develops, stabilizes, or declines over time. Future work should integrate behavioral, physiological, and cognitive measures. Playback studies in managed populations, combined with stress hormone assays or memory and discrimination tests, could reveal how giraffes encode, retain information on, and respond to predator cues. Moreover, it remains to be investigated how predator experience is acquired in giraffes, for example, whether through individual learning, repeated encounters, or social transmission from more experienced group members. In a conservation context, such work could inform predator conditioning protocols prior to reintroduction (Blumstein et al., 2019), ensuring that naïve giraffes can reacquire functional antipredator behaviors in changing landscapes of fear.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Ethics statement

The animal studies were approved by Animal Research Ethics Committee of the University of the Free State (UFS-AED2022/0045/23). The studies were conducted in accordance with the local legislation and institutional requirements. Written informed consent was obtained from the owners for the participation of their animals in this study.

Author contributions

AB: Methodology, Visualization, Investigation, Data curation, Software, Conceptualization, Writing – original draft, Resources, Writing – review & editing, Validation, Project administration, Supervision, Funding acquisition, Formal analysis. GS: Formal analysis, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2025.1634218/full#supplementary-material>

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