An Experimental Evaluation of Cheetah (*Acinonyx jubatus*) Reactions to Sound Playbacks of Domestic Animals and Correlations between Humans' Attitudes towards Carnivores and their Accuracy of Species Identification

By

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"If we can teach people about wildlife, they will be touched. Share my wildlife with me. Because humans want to save things that they love."

- Steve Irwin

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Introduction

Most populations of large carnivores are in decline [1, 2]. Those that remain often inhabit landscapes influenced by humans and their associated activities. For example, humans convert habitat to agriculture, construct fences and roads, partake in recreational activities, and graze livestock. These actions reduce habitat availability and increase interactions between carnivores and people. As a result, conserving large carnivores increasingly depends on promoting coexistence with humans [3-6]. However, coexistence presents significant challenges. Carnivores can threaten livestock and human safety [7, 8], while people often respond by killing carnivores preemptively or in retaliation [9-12]. Additionally, humans and their associated stimuli can negatively impact carnivore behavior, health, and reproductive success [13-19]. Addressing these challenges requires interdisciplinary research that examines how humans and their associated stimuli affect carnivore behavior, the risks carnivores pose to people, and the risks people pose to them. Such research is critical to informing management interventions that reduce negative outcomes for both parties, ultimately promoting coexistence.

Understanding how humans and their associated stimuli affect carnivore behavior necessitates examining how carnivores respond to domestic animals. Different types of livestock and breeds of domestic dogs are among the most common human-associated stimuli in carnivore habitats, often resulting in interactions and potential conflict. However, most knowledge about carnivore responses to domestic animals relies on indirect methods, such as correlating movement data with areas of domestic animal presence or broad assumptions that carnivores are attracted to (e.g., livestock) or deterred by (e.g., livestock guarding dogs) specific domestic animal types [14, 16, 20-28]. These approaches limit understanding of cause-and-effect relationships in carnivore-domestic animal interactions and the individual differences among carnivores that may influence outcomes. Domestic animals may deter carnivores if perceived as threatening or attract them if viewed as prey, with responses potentially differing between domestic animal types or individual carnivores. Given the significance of these effects, potentially leading to carnivore displacement, retaliatory persecution, domestic animal suffering, or economic losses, robust data on individual carnivore responses to interactions with domestic animals are needed to predict outcomes and inform management interventions confidently [29].

To address these challenges, we examine the short-term reactions of individual cheetahs (*Acinonyx jubatus*) to audio playbacks simulating two types of livestock (cattle and sheep/goats), two breeds of domestic dogs (livestock guarding dogs and non-livestock guarding dogs), and two control animals (hornbill and frogs) during randomized crossover trials. For each domestic animal type, we test contrasting hypotheses: Deterrence, predicting that cheetahs move away from the playback speaker, and Attraction, predicting that cheetahs move toward it. This approach allows us to draw robust inferences about the causes of attraction, deterrence, or neutral responses and how these responses may predict longer-term behaviors. For example, deterrence after livestock stimuli could suggest a low risk of livestock predation, while deterrence after dog stimuli may indicate that the presence of dogs can protect livestock. Conversely, attraction to any stimulus may signal an imminent predation risk and raise the likelihood of human retaliation against the individual or conspecifics that cross paths with the domestic animal's owner. If most cheetahs exhibit similar responses, our findings could provide broader insights applicable to other populations. Ultimately, this aims to deepen our understanding of how domestic animals affect cheetah behavior, identify the causes of livestock predation, and inform interventions that promote coexistence.

In addition to understanding carnivore behavior, examining how people pose risks to carnivores requires a different approach. Numerous studies attempt to identify individuals with negative attitudes toward carnivores to help predict who may be more likely to kill them [11, 30, 31]. However, in communities living among multiple carnivore species, each species is likely associated with distinct costs and benefits, such as varying risks to livestock or contributions to wildlife tourism [8, 32-36], which might influence species-specific attitudes. Alternatively, individuals may generalize their attitudes across species [37, 38]. One factor potentially influencing whether attitudes are species-specific or generalized is the ability to accurately identify species. Misidentification might lead to misapplied perceptions of costs and benefits, influencing attitudes and mortality risks for certain carnivores. Despite recognizing these factors, few studies have explored the relationship between identification ability and species-specific perceptions [39-41].

To address this, we surveyed community members near Kenya's Maasai Mara National Reserve to assess their perceptions of, and ability to identify, six native carnivore species: cheetahs, lions (*Panthera leo*), leopards (*Panthera pardus*), African wild dogs (*Lycaon pictus*), spotted hyenas (*Crocuta crocuta*), and striped hyenas (*Hyaena hyaena*). Using within-subject analysis, we tested three hypotheses: whether respondents hold species-specific or generalized perceptions (H1), whether identification ability correlates with perceptions (H2), and whether misapplied perceptions arise from misidentification (H3). By understanding how perceptions correlate with identification ability, we aim to make more nuanced predictions about species' risks of anthropogenic mortality and the need for species-specific or generalized management interventions. For example, if individuals perceive higher costs from species A but confuse species B with A, they may misapply those costs to B, leading to similarly negative attitudes and increased mortality risks for both species. Such misapplied perceptions could render species-specific management interventions inefficient, as actions aimed at mitigating the costs associated with species B might fail to address those attributed to A, for which B is blamed.

This research addresses novel questions relevant to various challenges of conserving large carnivores. By examining how cheetahs respond to domestic animals, we aim to uncover how different types of livestock and domestic dog breeds influence cheetah behavior. This approach could help identify the causes of livestock-related conflicts and evaluate whether different breeds of domestic dogs can protect livestock by deterring cheetahs. Cheetahs are particularly suitable for studying these dynamics. Due to their subordinate status among large carnivores, cheetahs may exhibit more nuanced responses to various domestic animals, offering insights into whether different domestic animal types elicit distinct behavioral effects. The experimental approach, involving direct observation and controlled audio playbacks, provides robust inferences by isolating key variables and enabling inter-individual comparisons, which are difficult to identify through correlations alone [42]. Simultaneously, examining correlations between people's perceptions of carnivores and their ability to identify species may improve predictions of who is more likely to kill specific species. Misidentifications could misapply perceptions of costs and benefits, shaping species-specific attitudes and mortality risks. Through this interdisciplinary research, we aim to inform management interventions that address the complexities of human-carnivore coexistence, protecting both people's livelihoods and carnivore populations.

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Chapter 1: Experimental Evaluation of the Behavioral Responses of Cheetahs (*Acinonyx jubatus*) to Livestock Vocalizations

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Abstract. Human activities, including livestock grazing, influence the behavior of large carnivores like cheetahs (*Acinonyx jubatus*). Most knowledge about these effects relies on indirect methods, such as correlating movement data with livestock-associated areas. This limits our understanding of cause-and-effect relationships of cheetah-livestock interactions, and inter-individual differences that may influence the outcomes. Livestock may deter cheetahs if perceived as threatening or attract them if viewed as prey, with responses potentially differing between cattle and smaller livestock like sheep and goats (shoats). Given the significance of deterrent or attractive effects, potentially causing displacement or preemptive retaliatory persecution of cheetahs, livestock suffering, and livestock losses for people, robust data on individual cheetah responses to interactions with different livestock types are needed to help predict the outcomes and inform management interventions. Here, we experimentally tested cheetah responses to audio playbacks simulating cattle, shoats, and a control animal during randomized crossover trials. We tested two hypotheses for cattle and shoats: *Deterrence*, predicting movement away from the playback speaker, and *Attraction*, predicting movement toward it. Most cheetahs moved after the cattle playback, and the majority of those moved away from the speaker, providing weak evidence for *Deterrence*. This suggests that interactions with cattle can cause short-term displacement in some cheetahs, potentially altering ranging patterns, increasing stress, reducing reproductive success, or leading to habitat exclusion if such interactions are frequent. In contrast, few cheetahs moved after the shoat playback, providing no evidence for Deterrence or Attraction. Thus, interactions with shoats are unlikely to cause significant behavioral changes but may instead influence cheetahs indirectly through habitat modification or prey availability. These findings highlight the importance of direct, experimental studies in understanding carnivore-livestock interactions and the variability in individual responses. Future research should investigate the duration and frequency of cattle-induced deterrent effects and assess how characteristics of classes of cheetahs, such as males versus females or singletons versus females with cubs, influence responses. Overall, our results suggest that cheetahs can coexist with both livestock types. However, livestock managers should consider the frequency of cheetah-cattle interactions and work to minimize the indirect effects of cattle and shoat presence. While addressing these indirect effects should help reduce conflict, incorporating additional non-lethal deterrence methods remains essential to mitigate livestock loss and promote coexistence.

Introduction

Understanding the effects of human activities on wild animal behavior is crucial for fostering coexistence, especially with large carnivores, which prey on domestic animals and can threaten personal safety. Examining how individual carnivores respond to interactions with livestock can guide interventions to minimize consequences for all parties, including human retaliation for livestock loss. However, predicting how individual carnivores respond to livestock presence is not always straightforward. Livestock may deter carnivores if they are perceived as threatening or if their presence is associated with humans or their non-lethal deterrents [1-8]. Conversely, livestock may attract carnivores if they are associated with food or seen as potential prey [2, 4]. Predicting how individual carnivores respond to livestock demands more data rather than a blanket assumption that livestock will die.

We lack direct observations of individual carnivore behavior during and after known interactions with livestock presence, especially when livestock stimuli have been experimentally manipulated. Instead, most studies report correlative data or indirect measures of behavior. For example, researchers use stationary cameras or GPS collars to correlate carnivore presence or movement with livestock-associated areas [2, 9-18]. However, because carnivores and livestock independently and simultaneously move through landscapes, these studies can rarely identify when carnivores encounter livestock or their stimuli. Consequently, they offer few explanations about whether observed effects were caused directly by interactions with livestock or indirect factors associated with their presence, such as altered prey availability or habitat suitability. Additionally, they rarely capture inter-individual differences among carnivores that can influence local risk of conflict with people, as some individuals may be more prone to livestock predation or pose a greater risk to human safety. Therefore, more robust data on individual carnivore responses following known interactions with experimentally manipulated livestock stimuli are needed to improve our ability to predict how they will respond [19].

Several recent studies have directly measured how large carnivores respond to known interactions with people or domestic animals, employing various methods under experimental and non-experimental conditions. For example, Ordiz et al. (2013) and Karlsson et al. (2007) used GPS collars to track the response of brown bears (*Ursus arctos*) and wolves (*Canis lupus*) when approached by people on foot [7, 8]. Landry et al. (2020) employed night-vision cameras to watch wolves following interactions with livestock guarding dogs (LGDs) and sheep [4]. Smith et al. (2007) and Suraci et al. (2019) used motion-triggered cameras at puma feeding sites to compare the responses of pumas (*Puma concolor*) to audio playbacks of humans, domestic dogs, or control sounds (frogs) [20, 21]. Additionally, Pangle and Holekamp (2010) and Maddox (2003) visually observed and compared the behavior of spotted hyenas (*Crocuta crocuta*) and cheetahs (*Acinonyx jubatus*) in response to audio playbacks of cowbells and controls, church bells and king penguins (*Aptenodytes patagonicus*), respectively [3, 22]. Though illuminating, several limitations of these studies have left gaps in our knowledge. Night-vision cameras in Landry et al.'s study only captured wolves after they approached sheep with LGDs [4], limiting insights about whether wolves respond differently to unexpected encounters, such as when sheep and LGDs approach without wolf initiation. Similarly, the hyena and cheetah studies only exposed individuals to isolated cowbell sounds rather than actual recordings from cattle herds [3], which would include vocalizations from the cattle and bell sounds. This suggests unfamiliar or novel stimuli could have triggered responses. To provide more robust inferences about the causes and effects of livestock encounters on individual carnivores, additional studies are needed that directly observe carnivore responses to stimuli closely simulating the livestock they are likely to encounter.

It might be useful to know whether the stimuli associated with livestock that precede physical interactions (e.g., sounds, smells, sight, etc.) produce deterrent, attractive, or neutral reactions. These effects are more likely to be revealed by directly observing individuals before and after the subject is exposed to the stimulus. Telemetry and GPS collars cannot capture short-term (seconds to minutes), fine-scale directional movement associated with rare interactions or changes in body posture and vigilance, which can more easily diagnose the stimulus's effect and salience (meaningfulness) [23-26]. Furthermore, while short-term reactions may not reveal longer-lasting effects, they provide a building block to understand longer-term behavior. For example, a subject that moves away shortly after exposure to livestock stimuli might continue moving for hours or even days, as demonstrated by Ordiz et al. (2013) with brown bears that continued avoiding the interactions sight after initially fleeing from approaching people [8]. Conversely, a subject that moves toward such stimuli in the seconds or minutes following its presentation might consistently be attracted to livestock and seek out interactions. However, direct observation requires carnivores habituated to human observation yet still responsive to novel, potentially salient stimuli associated with livestock.

Here, we observe the short-term reactions of individual cheetahs to audio playbacks of cattle and shoat (combined herds of sheep and goats) vocalizations and any associated bells, and a control animal, African grey hornbills (*Lophoceros nasutus*), presented during randomized crossover trials. We experimented in four wildlife conservancies surrounding Kenya’s Maasai Mara National Reserve, where the conditions are ideal due to the high density of individually identifiable cheetahs habituated to human observers in vehicles, and who may frequently encounter cattle, shoats, or hornbills [2, 27, 28].

We test contrasting hypotheses: *Deterrence*, predicting that cheetahs move away from the playback speaker, and *Attraction*, predicting that cheetahs move toward the playback speaker (Figure 1-1). Cheetahs have been observed spending more time moving in the first hour following playbacks of cowbells than following playbacks of king penguins (control condition) [22]. They also avoided stopping in areas with high livestock abundance and avoided permanent settlements, roads, agricultural areas, and livestock enclosures [2, 22, 29-32]. This suggests that if cheetahs perceive cattle or shoats as threatening or associate them with human threats, they may be deterred by cattle or shoat stimuli. However, one of the same studies also reported that cheetahs were more likely to stop in areas where livestock frequently graze [2]. Also, several studies reported that cheetahs killed livestock, especially smaller livestock like shoats [2, 33-35]. These suggest they may be attracted to livestock, particularly smaller livestock types, as prey. However, no published study has directly observed and compared the short-term reactions of individual cheetahs to the experimentally manipulated presence of multiple livestock types.

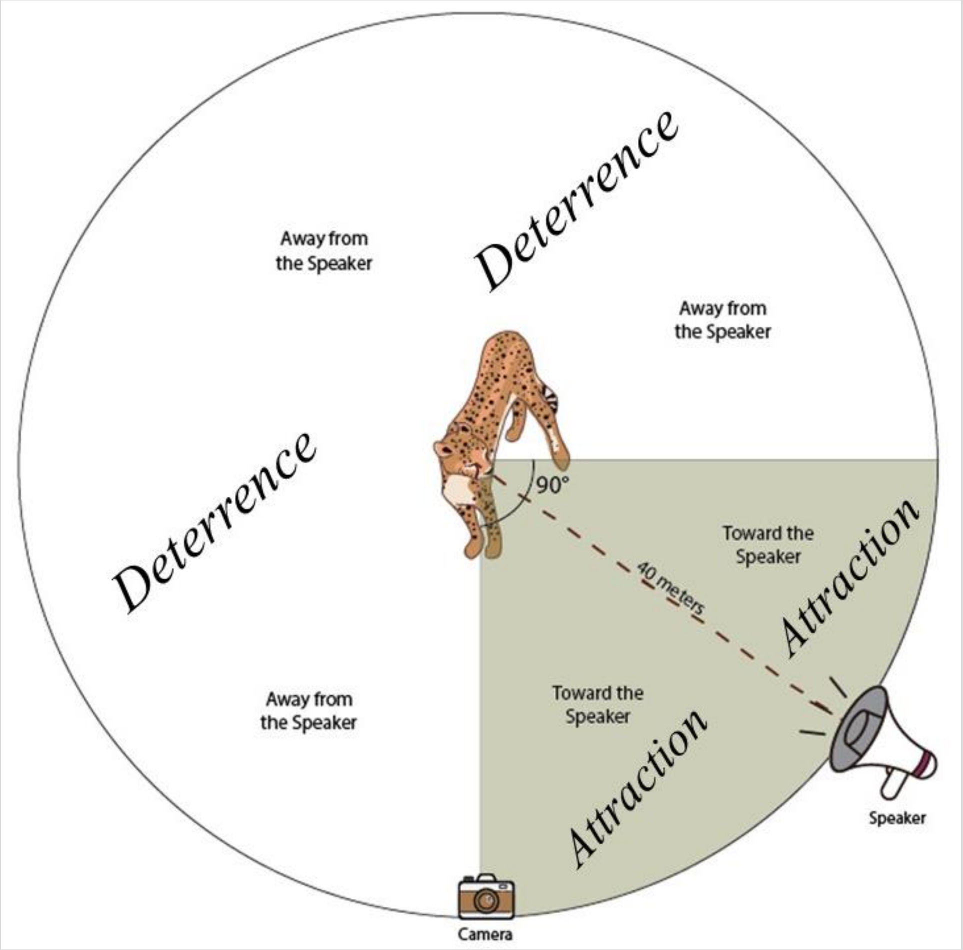

Figure 1-1: *Deterrence* would be supported if individuals move away from the speaker following the livestock playback. *Attraction* would be supported if individuals move toward the speaker following livestock playback. A subject moved toward the speaker when it moved within the gray arc (90° arc from the camera to the speaker and directly left or right of the subject). A subject moved away from the speaker when it moved in any other direction (white area). We recorded a subject as vigilant and measured the time spent vigilant when it visually scanned toward the speaker (gray arc). We did not measure time spent vigilant (scanning) in any other direction (white area).

To differentiate between *Deterrence* and *Attraction*, we measured two movement response variables for each cheetah subject following audio playbacks of cattle, shoats, or hornbills: the time between playback initiation and the subject's first movement (latency to initiate movement) and their net percent time moving away from or toward the playback speaker (Figure 1-1). *Deterrence* would be supported if individuals exhibit significantly more movement away from the speaker, while *Attraction* would be supported if individuals exhibit significantly more movement toward the speaker [36-38]. The null hypothesis would be supported if individual movement in response to either livestock playback is similar to their reaction to the hornbill playback or if individuals do not move in response to either livestock playback [21].

We test each playback's salience (i.e., meaning) by measuring individual changes in the percent time active and vigilant toward the speaker (Figure 1-1) before and after each playback. Changes in activity include adjustments in body posture, such as sitting, standing, and any movement (i.e., whenever the subject is not lying down). This broad definition of activity allows us to measure behaviors that may preclude movement and indicate an individual's intention to move, even among individuals who remain stationary. Meanwhile, changes in vigilance toward the playback speaker indicate heightened interest in the stimulus [23]. Therefore, while changes in activity and vigilance may not help distinguish between *Deterrence* and *Attraction*, they provide inferences about the meaningfulness of the playbacks. One strength of crossover trials such as ours is within-subject comparisons that control for inter-individual variability. Also, randomized crossover trials show the lowest rates of errors of common study designs in wildlife research [39]. We also use between-subjects comparisons to understand inter-individual differences in response to the same stimuli.

We offer robust inferences about the cause of attraction, deterrence, or neutral reactions by measuring cheetahs' short-term responses following experimental livestock stimuli. We report immediate reactions that may predict longer-term behaviors. For example, short-term deterrence may lead us to infer the risk of livestock predation is minimal from that individual but might explain longer-term individual displacement. Conversely, short-term attraction could predict imminent predation and human retaliation against that individual or conspecific unlucky enough to cross paths with the livestock owner, potentially explaining longer-term cheetah absence in a locale. If most cheetahs behave similarly, we might be able to generalize to other populations. Moreover, our findings may illuminate the limitations of prior studies. Short-term neutral reactions would suggest neither deterrence nor attraction, suggesting any observed effects of livestock presence on cheetahs from other studies may reflect indirect factors associated with livestock presence. Therefore, our results promise insights into the causes of conflict and inform interventions to promote coexistence.

Results

We observed 12 individual cheetahs during 32 audio playback trials simulating the presence of cattle, shoats, or hornbills. Ten trials used a cattle playback, ten used a shoat playback, and twelve used a hornbill playback. The duration subjects were observed after each playback (≤1 hour, or Post-Playback Period [PPP]) did not differ between treatment or control conditions (cattle: 14:28 [Interquartile range: 5:28–36:04]; shoat: 59:03 [IQR: 30:25–60:00]; hornbill: 50:43 [IQR: 15:51–60:00]; Kruskal-Wallis: $\chi2$ = 0.49, df = 3, p = 0.92). Thus, we infer none of our playbacks elicited flight by the majority of cheetahs, which would have ended our observations for that trial and shortened the PPP significantly.

Movement: We estimated cheetah movement to or away from the speaker by dividing the net percent time the subject moved away from or toward the speaker throughout the PPP by their latency to initiate movement following the playback. Negative movement response scores indicate quicker and longer movement away from the speaker, supporting *Deterrence*. Positive movement response scores indicate quicker and longer movement toward the speaker, supporting *Attraction*.

Across cheetah subjects, median movement response scores did not differ from zero (no movement) following treatment or control playbacks (Table 1-1). Additionally, neither within-cheetah nor between-cheetah comparisons of median movement response scores across treatment and control playbacks nor between cattle and shoat playbacks showed significant differences (Table 1-1).

Table 1-1: Comparisons of median movement response scores following cattle, shoat, and hornbill playbacks. Within-cheetah tests examine if individual movement response scores differed from zero after each playback. Within-cheetah comparisons of conditions examine the differences in movement response scores for individual cheetahs that received both conditions. Between-cheetah comparisons of conditions examine the differences in movement response scores for all cheetahs exposed to both conditions.

Stimulus, Response Variable	**Movement Response Score**		
Within-Cheetah Tests (n of individuals)	**Median (IQR)**	**V =**	**p =**
Cattle (n = 10)	0 (-0.37 to 0)	7	0.53
Shoat (n = 10)	0 (0 to 0)	0	0.18
Hornbill (n = 12)	0 (-0.01 to 0)	0	0.1
Within-Cheetah Comparisons of Conditions (n of individuals)	**Difference in Median (IQR)**	**W =**	**p =**
Cattle vs. Hornbill (n = 10)	0 (-0.34 to 0)	10	0.67
Shoat vs. Hornbill (n = 10)	0 (0 to 0)	10	1
Cattle vs. Shoat (n = 9)	0 (-0.11 to 0)	7.5	0.61
Between-Cheetah Comparisons of Conditions	**Difference in Median**	**W =**	**p =**
Cattle vs. Hornbill	0	4	0.11
Shoat vs. Hornbill	0	5	0.86
Cattle vs. Shoat	0	4	0.26

We included the median and interquartile range (IQR: 1st to 3rd quartile) of individual movement response scores for within-cheetah tests and comparisons.
We analyzed within-cheetah movement response scores using Wilcoxon signed-rank tests.
We analyzed within-cheetah comparisons using the Hills-Armitage approach [40] and Wilcoxon rank sum tests, excluding individuals who received only one playback.
We analyzed between-cheetah comparisons using Wilcoxon rank sum tests.

Most individuals moved following the cattle playback (n = 6 of 10), with four exhibiting net movement away from the speaker and two exhibiting net movement towards it (Figure 1-2). All four individuals who moved away from the speaker fled the trial location, ending their PPP, while the two who moved towards it remained in views throughout their PPP. In contrast, only three of ten individuals moved following the shoat playback, and four of twelve moved following the hornbill playback, all moving away from the speaker (Figure 1-2). Two individuals who moved following the shoat and hornbill playbacks, respectively, fled the trial location, while the rest remained in view throughout their PPP. Additionally, individuals spent more time moving away from the speaker after the cattle playback (mean ± SE: -6% ± 4) and had a shorter latency to move (28:44 min:sec ± 8:57) than after the shoat (net movement: -4% ± 3%; latency: 49:24 ± 5:26) or hornbill playbacks (net movement: -2% ± 2%; latency: 49:28 ± 5:10; Figure 1-2). Although statistical tests comparing individual net movement (Wilcoxon signed rank test, V = 10, p = 0.55) and latency to move (V = 5, p = 0.15) following the cattle and hornbill playbacks were insignificant, the effect sizes suggest that the cattle playback influenced some cheetahs. Given the greater movement away from the speaker, these results provide some evidence for *Deterrence* in the case of cattle.

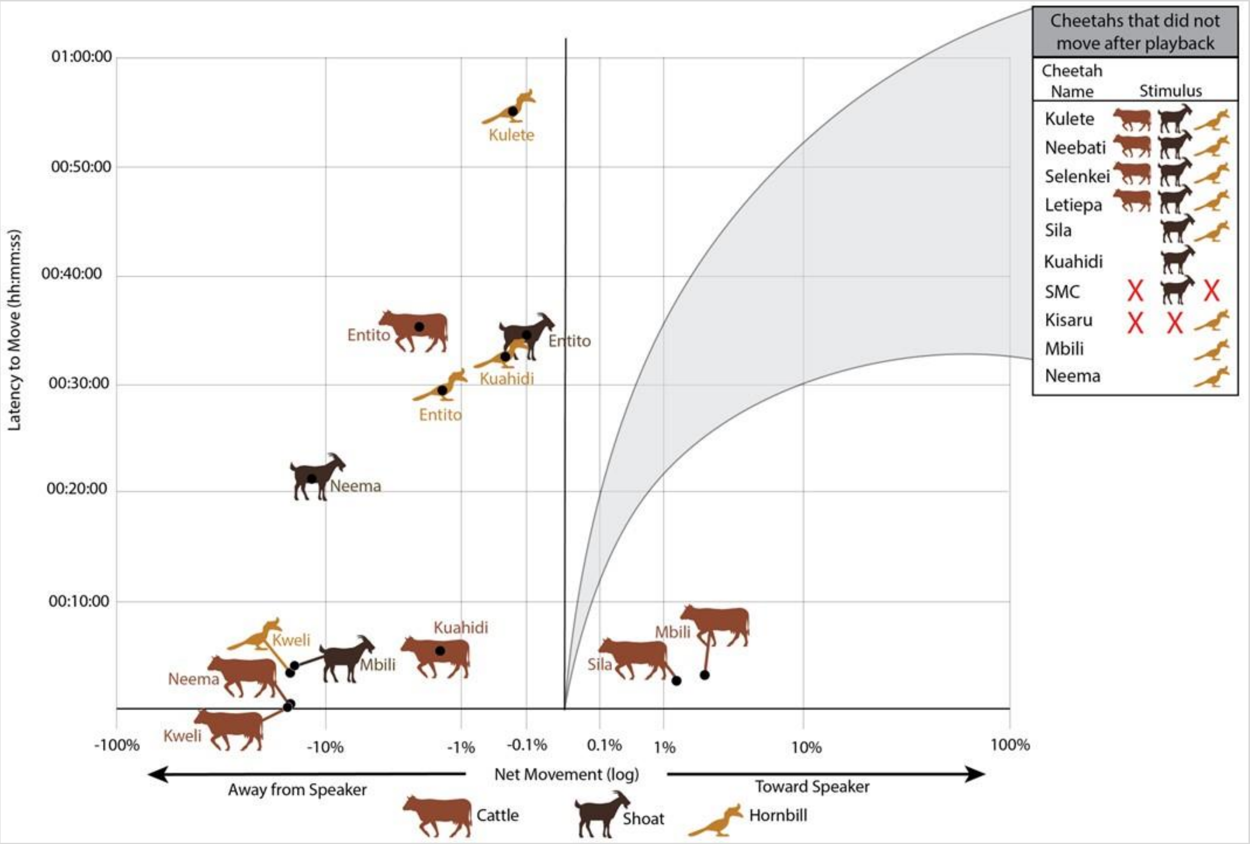

Figure 1-2: Cheetah movements following audio playbacks of cattle (brown), shoats (dark brown), or hornbills (yellow). Individual cheetahs (circles with names), net percent time moving away from or toward the speaker (x-axis), and latency to move (y-axis) after each playback. Individuals on the left of the graph exhibited net movement away from the speaker, while individuals on the right exhibited net movement toward the speaker. Individuals who did not move after each playback are listed in the box in the top right. Red Xs in the box indicate that individual was not exposed to that playback.

Activity: We measured each cheetah's change in activity (sitting, standing, walking, or engaging in other fast-paced movements) following each playback across two timeframes: consecutive five-minute post-playback intervals (PPIs: PPI 1 = 0–5 min, PPI 2 = 5–10 min, etc.) and the entire post-playback period (PPP). For each timeframe, we calculated the change in percent time active by subtracting the percent time active during the initial observation period (IOP = -5 to 0 min before playback) from each PPI and the PPP.

Cheetahs exposed to cattle or shoats were generally more active during PPI 1 than during the IOP (Table 1-2, Figure 1-3). However, within-cheetah tests indicated these changes were insignificant following cattle and only suggestive following shoats (Table 1-2). Those exposed to hornbills showed no activity change during PPI 1 (Table 1-2, Figure 1-2). While some subjects maintained higher activity levels during PPI 2 following cattle or shoat playbacks, no statistical differences were found (Table 1-2), suggesting most had returned to baseline (IOP) activity levels. Therefore, activity was not analyzed during subsequent PPIs.

Table 1-2: Comparisons of the changes in activity and vigilance toward the speaker following cattle, shoat, and hornbill playbacks. Within-cheetah tests examine if individuals exhibited an increase in either behavior during post-playback intervals (PPIs) or throughout the post-playback period (PPP) after each playback than during the initial observation period (IOP). Within-cheetah comparisons of conditions examine the differences in each behavior for individual cheetahs that received both conditions. Between-subject comparisons of conditions examine the differences in each behavior for all cheetahs exposed to both conditions.

Stimulus, PPIs, PPP / Behavior		**Activity**			**Vigilant Toward the Speaker**		
Within-Cheetah Tests After vs. IOP (n of individuals)		**Median % (IQR)**	**V =**	**p =**	**Median % (IQR)**	**V =**	**p =**
Cattle	**PPI 1** (n = 10)	+14 (0 to +52)	0	0.06	+36 (+19 to +50)	0	0.002**
	PPI 2 (n = 7)	0 (0 to +8)	3	0.37	+2% (-1 to +11)	19	0.47
	PPP (n = 10)	+25 (+1 to +52)	0	0.02*	+15 (+6 to +37)	3	0.01**
Shoat	**PPI 1** (n = 10)	+50 (0 to +78)	0	0.04*	+38 (+18 to +49)	0	0.002**
	PPI 2 (n = 9)	+12 (0 to +18)	1	0.06	+1 (-1 to +4)	18	0.63
	PPP (n = 10)	+24 (+4 to +42)	0	0.01**	+7 (+1 to +12)	8	0.05*
Hornbill	**PPI 1** (n = 12)	0 (0 to 0)	1	0.4	+3 (-2 to +18)	19	0.13
	PPP (n = 12)	+1 (0 to +3)	5	0.08	+2 (-1 to +10)	19.5	0.14
Within-Subject Comparisons of Conditions		**Difference in Median % (IQR)**	**W =**	**p =**	**Difference in Median % (IQR)**	**W =**	**p =**
Cattle vs. Hornbill	**PPI 1** (n = 10)	+1 (0 to +23)	19.5	0.16	+20 (+15 to +34)	25	0.008**
	PPI 2 (n = 7)	0 (0 to +9)	10.5	0.11	+1 (-6 to +4)	7	0.86
	PPP (n = 10)	+2 (-1 to +13)	19	0.2	+14 (+4 to +22)	21	0.09

Shoat vs. Hornbill	**PPI 1** (n = 10)	+20 (-1 to +36)	19.5	0.05*	+36 (-1 to +50)	18	0.11
	PPI 2 (n = 9)	+2 (0 to +15)	14	0.24	+1 (-2 to +9)	8	0.9
	PPP (n = 10)	+11 (-1 to +36)	18	0.12	+2 (-1 to +7)	12	0.8
Cattle vs. Shoat	**PPI 1** (n = 9)	-10 (-39 to 0)	8	0.73	+4 (-16 to +13)	10	1
	PPP (n = 9)	-2 (-34 to +3)	5	0.26	+12 (-7 to +20)	12	0.73
Between-Subject Comparisons of Conditions		**Difference in Median %**	**W =**	**p =**	**Difference in Median %**	**W =**	**p =**
Cattle vs. Hornbill	**PPI 1**	+14	38.5	0.11	+33	15	0.002**
	PPI 2	0	36.5	0.59	+3	33.5	0.5
	PPP	+12	39.5	0.18	+13	34.5	0.1
Shoat vs. Hornbill	**PPI 1**	+51	28	0.02*	+35	17	0.003**
	PPI 2	+12	46	0.32	+2	49	0.75
	PPP	+23	34	0.09	+5	51	0.57
Cattle vs. Shoat	**PPI 1**	-41	37	0.32	-2	51	0.97
	PPP	-11	48.5	0.94	8	66	0.25

Sample sizes varied between PPI 1 and PPI 2 for cattle and shoat playbacks due to the PPP ending during PPI 1 in some trials (see methods).
We did not test median behavior changes in PPI 3 for cattle and shoat playbacks or in PPI 2 for the hornbill playback, as prior PPIs showed no statistical changes in either behavior.
We analyzed within-cheetah tests using Wilcoxon signed-rank tests.
We analyzed within-cheetah comparisons of conditions using the Hills-Armitage approach [40] and Wilcoxon rank sum tests, excluding individuals who received only one playback.
We analyzed between-cheetah comparisons of conditions using Wilcoxon rank sum tests.
** Bonferroni corrections signifying a significant behavior change, $p \leq 0.01$.
* Bonferroni corrections signifying a suggestive behavior change, $0.05 \geq p > 0.01$.

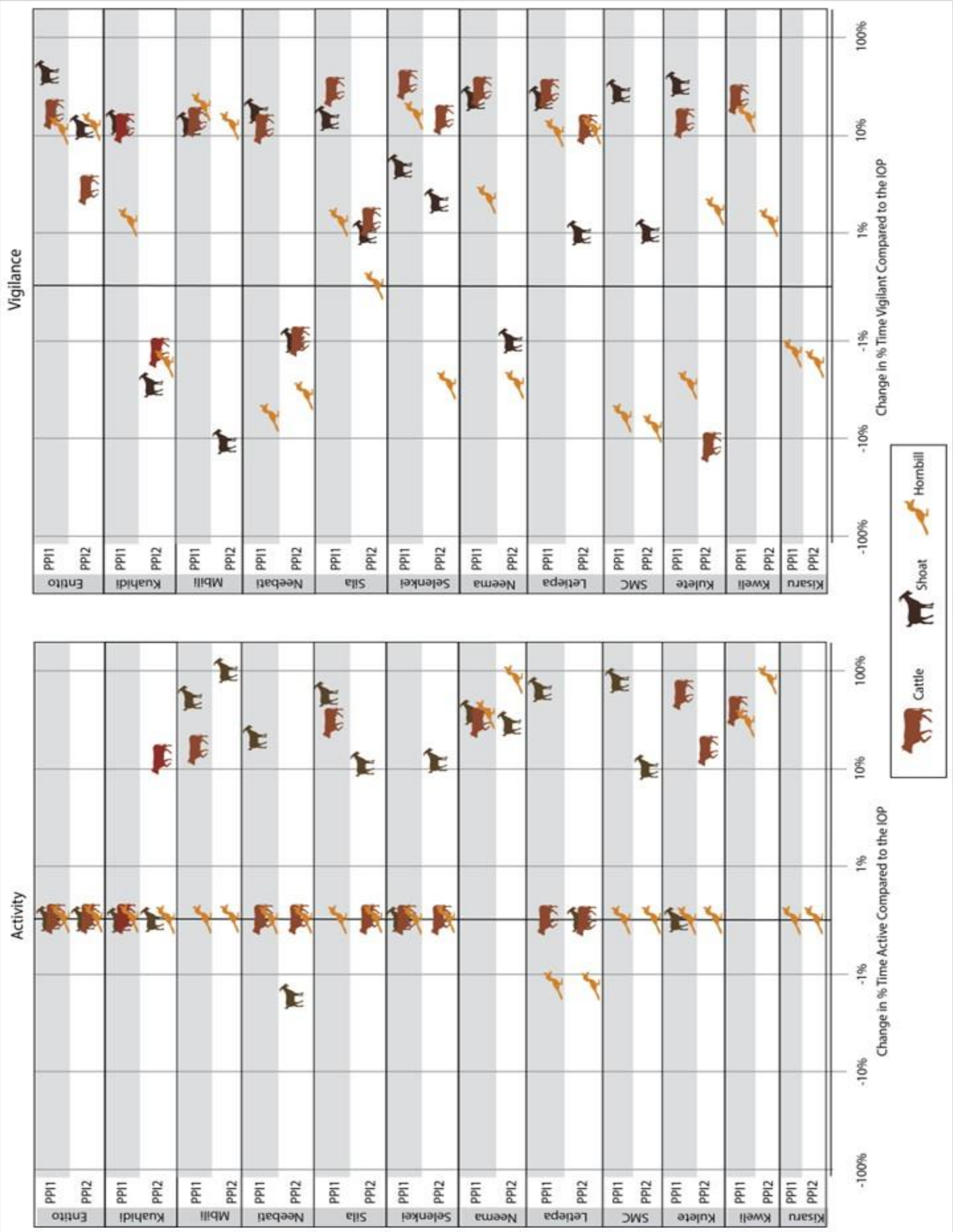

Figure 1-3: Individual changes in activity (left frame) and vigilance toward the speaker (right frame) between post-playback interval 1 (PPI 1) and 2 (PPI 2) and the initial observation period (IOP) after the cattle (brown), shoat (dark brown), or hornbill (hornbill) playbacks. A positive change indicates that the individual exhibited that behavior more during that PPI than during the IOP. A negative change indicates that the individual exhibited that behavior more during the IOP than the PPI.

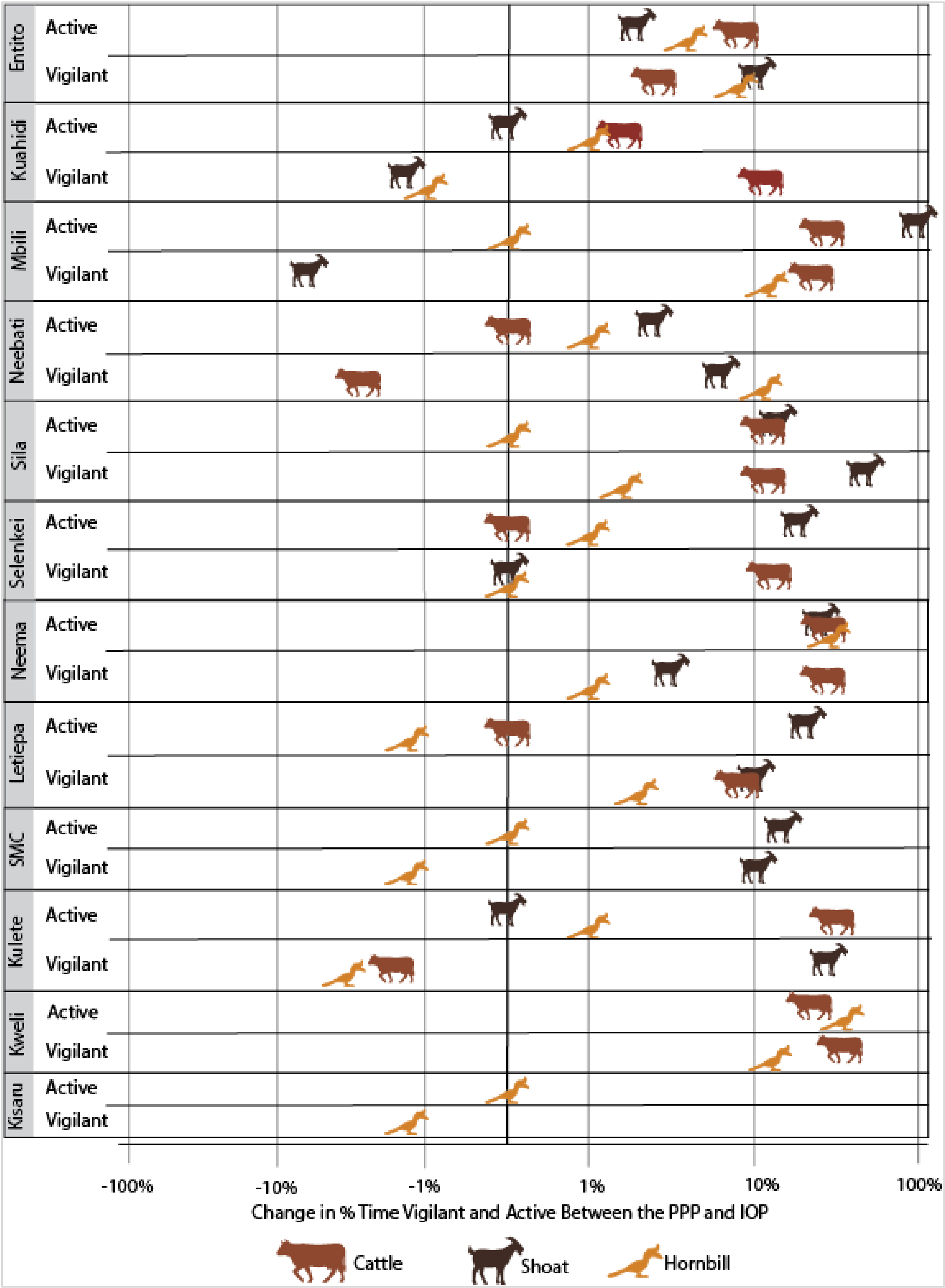

Figure 1-4: Individual changes in vigilance toward the speaker and activity between the post-playback period (PPP) and Initial Observation Period (IOP) after the cattle (brown), shoat (dark brown), or hornbill (yellow) playbacks. A positive change indicates that the individual exhibited that behavior more during the PPP than during the IOP. A negative change indicates that the individual exhibited that behavior more during the IOP than the PPP.

Comparisons of activity changes following different playbacks align with our initial findings. In PPI 1, cheetahs exposed to both cattle and hornbills, and all those exposed to either, were more active after cattle, though these differences were not statistically significant (Table 1-2; Figure 1-3). Cheetahs exposed to shoat and hornbills, and all those exposed to either, were more active after shoats, with within-subject tests indicating a suggestive difference and between-subject tests indicating a strong significant difference (Table 1-2; Figure 1-3). No significant differences in activity change were found when comparing the two livestock playbacks (Table 1-2). In PPI 2, no statistical differences in activity change were observed following cattle, shoats, or hornbills (Table 1-2), supporting our initial observation that subjects had returned to baseline activity levels by this interval.

Cheetahs remained more active throughout the PPP than during the IOP following cattle and shoats, with within-cheetah tests indicating a suggestive increase for cattle and a strong significant increase for shoats (Table 1-2, Figure 1-4). In contrast, those exposed to hornbills showed no increase in activity between these periods (Table 1-2, Figure 1-4), suggesting that the livestock playbacks induced persistent changes in activity that were not apparent when examining individual PPIs in isolation. However, comparisons within and between cheetahs revealed no significant differences in activity changes across cattle and hornbill, shoat and hornbill, or cattle and shoat playbacks (Table 1-2), indicating that individual and grouped activity changes were insignificant relative to the control stimuli.

Vigilance: Within-cheetah tests found individuals exposed to cattle or shoats were significantly more vigilant toward the speaker during PPI 1 than during the IOP, whereas those exposed to hornbills showed no change in vigilance between these periods (Table 1-2, Figure 1-3). During PPI 2, most individuals exposed to either livestock playback returned to baseline vigilance levels, with some exhibiting even less vigilance than during the IOP (Table 1-2; Figure 1-3). Consequently, vigilance was not analyzed during subsequent PPIs.

Comparisons of vigilance change following different playbacks align with our initial findings. In PPI 1, cheetahs exposed to cattle and hornbills and all individuals exposed to either showed significantly higher vigilance after cattle (Table 1-2, Figure 1-3). Similarly, cheetahs exposed to shoats and hornbills and all those exposed to either were more vigilant following the shoats, though only between-cheetah tests indicated a strong significant difference (Table 1-2, Figure 1-3). No significant differences in vigilance change were found between the two livestock playbacks (Table 1-2). In PPI 2, no statistical differences in vigilance change were observed following any of the playbacks, supporting our initial observation that most individuals had returned to baseline vigilance levels by this interval.

Cheetahs remained more vigilant throughout the PPP than during the IOP following both cattle and shoats, with within-cheetah tests indicating a strong significant increase for cattle and a suggestive increase for shoats (Table 1-2; Figure 1-4). In contrast, those exposed to hornbills showed no increase in vigilance between these periods (Table 1-2, Figure 1-4), suggesting that the livestock playbacks induced persistent changes in vigilance that were not evident when examining individual PPIs in isolation. However, within- and between-cheetah comparisons revealed no significant differences in vigilance changes across cattle and hornbill, shoat and hornbill, or cattle and shoat playbacks (Table 1-2), indicating that individual and grouped vigilance changes were not significant relative to the control stimuli.

Habituation and Order Effects: Individuals exhibited similar changes in activity and vigilance, regardless of the number of playbacks they were exposed to (Appendix 1: Habituation). Individual and grouped comparisons revealed that both individual cheetahs and groups of cheetahs exhibited similar changes in activity and vigilance following the cattle or shoat playback, irrespective of the order in which they were exposed to each (Appendix 2: Order-Effects). Therefore, we found no evidence of habituation or order effects.

Discussion

We tested two contrasting hypotheses – *Deterrence* and *Attraction* – to determine whether wild cheetahs are deterred by or attracted to cattle or shoats. To assess these hypotheses, we directly observed individual cheetahs' short-term responses to audio playbacks simulating the presence of cattle, shoats, and neutral animals (i.e., hornbills). Our findings suggest both livestock playbacks were salient, as cheetahs exhibited greater activity and vigilance after both. Individuals exhibited particularly pronounced responses in the first five minutes after both livestock playbacks, with significantly more vigilance observed after the cattle and significantly more activity observed after the shoat than after the hornbill playback. Despite this initial arousal, only six of ten cheetahs moved after the cattle playback, with just four moving away from the speaker (Figure 1-2). In contrast, most cheetahs remained stationary after the shoat (n = 7 of 10) and hornbill playbacks (n = 8 of 12; Figure 1-2). Consequently, our results provide only some evidence for *Deterrence* in the case of cattle and little evidence for *Attraction*. However, inter-individual differences among cheetahs were noted throughout, with some cheetahs attracted to and a larger number moving away from our cattle playbacks.

Two of our behavioral measures, activity and vigilance, offer insights into the salience of our playbacks and the extent of arousal in individual cheetahs. Vigilance reflects individuals gathering information and is a low-cost response requiring minimal physical adjustment [23, 26, 41-44]. In contrast, changes in activity, such as shifts in body posture or movement, require greater energy expenditure and make a cheetah more conspicuous to potential observers [24, 45]. Therefore, while increases in either vigilance or activity indicate a playback salience, heightened activity likely signals a higher level of arousal than vigilance alone. For example, a resting cheetah may only change its activity level if the playback is sufficiently salient to warrant a higher-cost response. However, changes in these behaviors do not necessarily reveal whether cheetahs perceive the playbacks as potentially threatening or beneficial. Specific behavioral patterns may offer further clarification. Cheetahs exhibiting increased vigilance while active (e.g., sitting, standing, or moving) have been correlated with a greater frequency of hunting [43], suggesting that this behavioral pattern may indicate individuals perceive a potential benefit from the playback stimulus. Conversely, cheetahs exhibiting increased vigilance while inactive (e.g., lying down) have been described as acting uneasy [43], suggesting such individuals perceive a potential threat. Therefore, while these behavioral measures cannot definitively distinguish *Deterrence* and *Attraction*, comparing how they change following each playback and whether they persist beyond an initial reaction provides valuable data on individual responses.

Ultimately, individual movement is the most informative indicator of *Deterrence* or *Attraction*. Movement is a high-cost behavior, requiring relatively higher energy expenditure and potentially exposing individuals to observers. Such risk might come from the stimulus (e.g., humans with livestock) or other nearby threats. Previous research on carnivores, including cheetahs, has used movement away from a speaker to infer deterrence in response to playbacks of known threats [21, 22, 45, 46]. Conversely, movement towards the speaker after playbacks of prey by other carnivore species, such as lions and hyenas, has been interpreted as attraction [36, 37, 47, 48]. While no prior study, to our knowledge, has simultaneously measured potential movements both away from and towards a speaker in response to stimuli of unknown value (i.e., threat or benefit), our approach enabled us to differentiate between these responses. When combined with changes in vigilance and activity, our observations provide nuanced interpretations along a spectrum of arousal levels elicited by each playback.

Cattle: A larger proportion of cheetahs moved after the cattle (n = 6 of 10) than after the hornbill playback (n = 4 of 12), suggesting more individuals perceived the potential presence of cattle as sufficiently salient to justify moving (Table 1-1). Furthermore, the movements away from the speaker by Entito, Kuahidi, Kweli, and Neema provide evidence for *Deterrence*: three individuals either did not move following the hornbill playback (Neema) or exhibited notably shorter latencies to move after the cattle (Kuahidi and Kweli; Figure 1-2). Additionally, all four fled from the observers' view during their observation periods after the cattle playback, whereas only Kweli and Entito did so after the hornbill (Figure 1-2). These findings align with an unpublished study that observed cheetahs moving more frequently in the first hour after an audio playback of cowbells compared to a king penguin control [22]. However, unlike the latter study, our cattle playbacks were recorded from herds our subjects could encounter rather than isolated cowbells, and our control playbacks were of a native animal presumed to be neutral. Combined with our observations of individual responses to both playbacks, which enabled within-subject comparisons, our data provides more robust evidence that the presence of cattle can directly cause *Deterrence,* at least in some individuals.

Several factors could explain why cattle might deter some cheetahs. As specialized hunters reliant on maintaining physical health to capture prey, cheetahs are particularly susceptible to injury that might prevent successful chase. Consequently, they are deterred by larger carnivores, even after making a kill, which they typically relinquish rather than defend at the risk of injury [45, 49-51]. Cheetahs may similarly perceive cattle as a direct threat to their safety because adult cattle can injure them or because humans or dogs may accompany the cattle. However, we have no evidence or anecdotal knowledge of cattle injuring or killing adult cheetahs. Thus, we suggest that deterrence might stem from caution around any animal too large or potentially dangerous to be considered prey. For example, during this study, we observed two cheetahs – Kulete and Leteipa – moving away from warthogs and giraffes, though these movements were not abrupt; the cheetahs seemed to move more out of inconvenience, often waiting for the warthog or giraffe to approach again before moving further. Additionally, rangers in the Maasai Mara conservancies have reported buffalo, a wild herbivore similar to cattle, killing cheetah cubs, which could lead mother cheetahs to associate cattle with a similar risk. While three of the cheetahs that moved away from the speaker after the cattle playback – Entito, Kweli, and Neema – had cubs, two others with cubs – Kulete and Neebati – did not move, offering inconsistent support for this explanation. Alternatively, cheetahs may associate cattle with human or domestic dog presence, both of which have directly injured or killed cheetahs [52-54]. Although our playbacks were designed to isolate whether cattle themselves deter cheetahs, people always accompany herds of cattle in the conservancies, and domestic dogs are common around settlements and with livestock herds along the conservancy peripheries [55]. Therefore, cattle's association with other human-related stimuli may be enough to trigger deterrence. Future research should explore how cheetahs respond to these associated human stimuli independently and together to understand better how the presence of each may influence deterrence. If people or dogs influence deterrence, managers could limit or recommend their presence, depending on whether they want cheetahs to be deterred.

Although we found some evidence for *Deterrence*, the lack of movement by four individuals and the movement toward the speaker by two others after the cattle playback suggest the effect was not uniform across individuals. Comparisons of our additional response measures, activity and vigilance, suggest cattle did cause greater arousal than hornbills and provide further insights into how individuals may have perceived the presence of cattle. For example, all four individuals that did not move after the cattle playback – Kulete, Leteipa, Neebati, and Selenkei – were more vigilant in the first five minutes compared to the same period after the hornbill (Figure 1-3), while Selenkei sustained greater vigilance throughout her observation period (Figure 1-4). In addition, three of the four – Leteipa, Neebati, and Selenkei – remained inactive (Figure 1-4). While this evidence lacks the detail to decipher whether these individuals perceived the cattle playback as potentially threatening or beneficial, we would describe these individuals as acting somewhat erratic and uneasy after the cattle playback, aligning with previous descriptions of cheetahs displaying similar behavioral patterns [43]. As a result, we interpreted their increased vigilance and inactivity as an attempt by these individuals to detect a potential threat while minimizing their chance of exposure.

The movement toward the speaker by Sila and Mbili in the first five minutes after the cattle playback suggests some evidence for *Attraction*, suggesting they may have perceived cattle presence as beneficial. This interpretation is supported by their greater vigilance during this period compared to the hornbill playback, aligning with Caro's (1987) correlation of increased vigilance while active with a higher likelihood of hunting [43]. However, some evidence indicates that cheetahs prefer wild prey over livestock and tend to kill smaller livestock like sheep and goats [56-60], likely due to their size. Thus, it is unlikely they perceived cattle themselves as prey. If they had, we might have expected similar or greater movement toward the speaker after the shoat playback, which was not observed in these or any other cheetahs. A more plausible explanation for their movement could be the potential for cattle to flush out wild prey, aiding hunting, or a need to assess cattle as a possible threat. Though we did observe one cheetah hunt an impala potentially flushed by a domestic dog playback (not discussed in this chapter), we observed no prey flushed by livestock playbacks. After their initial approach, Sila and Mbili returned to their original locations, laid down, and remained inactive while maintaining greater vigilance than after the hornbill playback, suggesting they continued monitoring for cattle presence. Their post-approach behavior mirrored that of cheetahs who did not move away from the speaker, possibly indicating a minimal perceived threat. If they perceived cattle as a low-level threat, they might have initially approached to watch for flushed prey but, upon finding none, returned to their original locations and continued monitoring for potential danger. Without more detailed behavioral data, it remains challenging to interpret their responses to the cattle playback precisely. Given that some individuals may perceive cattle presence as potentially beneficial, additional observations of cheetahs responding to cattle could clarify whether they perceive cattle as potential prey, a hunting aid, or a threat.

Observations of individual cheetah responses to the cattle and hornbill playbacks revealed markedly varied reactions. While the available evidence suggests that cheetahs likely perceived the presence of cattle as threatening, their diverse responses indicate different individuals may perceive a different threat level, sufficient to deter some while prompting others to investigate, either by remaining stationary but vigilant or briefly moving toward the source. Several factors could influence these varied responses, such as individual temperament or past experiences. For example, Maddox (2003) found that cheetahs with more presumed experience encountering cattle moved less in the hour following cowbell playbacks than those with less presumed experience [43]. Thus, familiarity with cattle might modulate cheetah reactions. We could not estimate the experience levels of our subjects, as all cheetahs in our study area are likely to encounter cattle. Alternatively, habitat type could influence perceived threat levels; cheetahs in open habitats might feel more exposed and, therefore, perceive a greater threat, while those in dense habitats might perceive a greater threat due to an inability to confirm the absence of cattle [61]. Conversely, individuals in dense habitats may feel more secure, leading to lower vigilance. Future research should explore how individual backgrounds, prior encounters with cattle, and other contextual factors shape cheetah responses. Insights from such studies could help develop management strategies that support cheetahs in adapting to cattle presence, potentially reducing or increasing deterrent effects, depending on the desired outcome.

Shoats: A smaller proportion of cheetahs moved after the shoat (n = 3 of 10) compared to the hornbill playback (n = 4 of 12), suggesting that most individuals did not perceive our simulated presence of shoats as sufficiently salient to justify moving. The three cheetahs that did move after the shoat playback – Entito, Mbili, and Neema – all moved away from the speaker (Figure 1-2), providing some evidence for *Deterrence*. However, their responses were generally weaker than their reactions to cattle and similar to their reactions to hornbills. For example, Entito exhibited delayed movement away from the speaker after all three playbacks (shoat: 34:41; cattle: 35:34; hornbill: 29:42) but laid back down and remained in view of the observer throughout her observation period following the shoat playback, whereas she fled from view after both the cattle and hornbill playbacks. Neema exhibited a longer latency to move after the shoat (27:12) than after the cattle playback (00:56) and did not move after the hornbill. Meanwhile, while Mbili moved away from the speaker after the shoat and toward the speaker after the cattle, he was more vigilant in the first five minutes and throughout his observation period after hornbills and cattle than after shoats. Therefore, his movement after the shoat playback may reflect a weak deterrent effect; his lack of vigilance indicates a lack of concern or interest in the presence of shoats, suggesting the direction of his movement after the shoat playback may have been random. These responses, combined with the lack of movement by most individuals, align with a previous study that found shoat playbacks did not deter badgers [62]. However, to our knowledge, this is the first experimental evidence demonstrating that the presence of shoats is unlikely to deter or attract a large carnivore directly.

While most cheetahs did not move after the shoat playback, comparisons of changes in activity and vigilance suggest shoats did cause greater arousal than hornbills. Kuahidi and Kulete exhibited the weakest responses, with both remaining lying down after the shoat playback (Figure 1-4). Additionally, although both were more vigilant in the first five minutes after shoats than after hornbills (Figure 1-3), only Kulete maintained higher vigilance throughout her observation period (Figure 1-4). While this behavioral pattern suggests both Kuahidi and Kulete more likely perceived the presence of shoats as potentially threatening [43], requiring an initial investigation by both individuals, it also suggests Kulete may have perceived a greater threat, requiring a persistent investigation. Three other cheetahs – Leteipa, Neebati, and Sila – showed stronger behavioral responses, characterized by greater vigilance in the first five minutes after shoats than after hornbills (Figure 1-3), followed by a return to similar rates of vigilance for the remainder of their observation periods (Figure 1-4). This was accompanied by greater activity in the first five minutes and throughout their observation periods after shoats. Because we only measured vigilance directed at the speaker (Figure 1-1), their return to baseline levels of vigilance while remaining active may indicate that these individuals redirected their attention away from the speaker after failing to confirm shoat presence in the first five minutes visually. This broader pattern of scanning while active could reflect a hunting response [43], implying that they perceived the presence of shoats as potentially beneficial, either viewing the shoats themselves as prey or as a means of flushing out wild prey.

Alternatively, this pattern could also indicate a response to a perceived threat, with scanning in other directions to monitor for danger and increased activity reflecting readiness to move if necessary. Finally, Sila's adult cub (SAC) exhibited the strongest and most consistent behavioral response, exhibiting greater vigilance and activity in the first five minutes and throughout his observation period after the shoat than after the hornbill playback (Figures 1-3 & 1-4). This sustained response suggests that SAC perceived the presence of shoats as meaningful enough to warrant continuous monitoring and readiness. SAC's recent dispersal from his mother might have contributed to this heightened response due to his inexperience with shoats, making him more cautious in unfamiliar situations. While anecdotal evidence by employees at the Mara Predator Conservation Programme (MPCP) suggests recently dispersed cheetahs may kill more shoats due to less honed hunting skills, they might also show increased caution in new contexts. SAC's response could, therefore, reflect a perception of shoats as either a potential threat or benefit, but without movement, we can't distinguish *Attraction* from *Deterrence* or some third option. Overall, these varied responses highlight the complexity of cheetah behavior toward shoats. While initial vigilance was common, the lack of significant movement suggests that individuals did not perceive the presence of shoats as sufficiently threatening or beneficial to prompt further action.

While we provide the first direct observations of individual cheetahs responding to shoats, our lack of support for attraction aligns with studies suggesting cheetahs prefer wild prey when available [56].

Moreover, while we have no direct evidence that cattle pose a more significant threat to cheetahs, our study offers the first indication that different livestock may elicit different behavioral responses. A likely explanation for why shoats do not deter cheetahs, while cattle might, is their difference in size. Shoats are significantly smaller than cattle and closer in size to the preferred prey of wild cheetahs. If cattle deter cheetahs due to their size, individuals may not feel the same caution around shoats, indirectly supported by cheetahs being more likely to kill shoats, indicating they are perceived as less threatening. Other factors, such as differences in grazing practices, might also explain this difference. Although herds of cattle and shoats are grazed with similar methods in the Maasai Mara, including associated people or domestic dogs, people may be more defensive of cattle for cultural or economic reasons. That could lead to more frequent confrontations that make cheetahs more cautious around cattle.

Broader Implications: Our findings of short-term deterrence by cattle suggest significant implications for cheetah ecology and conservation, as displacement following cattle interactions could lead to varying outcomes depending on their frequency and severity. Frequent and prolonged interactions may force cheetahs into continuous movement, potentially leading to exclusion from high-density cattle areas. This aligns with previous research demonstrating that cheetahs move faster and stop less in areas with the highest livestock abundance (cattle and shoats) [2]. In severe cases, this could result in complete avoidance of these regions, shrinking their available habitat and risking local extirpation.

Consistent deterrence may also impact individual health and increase risk even in less extreme scenarios. For example, elevated cortisol levels in transient male cheetahs indicate stress, which could affect long-term health [63]. Moreover, since cattle are predominantly active during the day, frequent interactions could limit cheetahs' daytime activities, forcing them into hiding or constant avoidance, increasing their reliance on nighttime activity when larger threatening carnivores are more active. Conversely, if cattle interactions are infrequent or deterrent effects are short-lived, the impact on cheetah behavior may be minimal. Cheetahs have shown adaptability to frequent short-term deterrence by avoiding threatening large carnivores during interactions rather than employing proactive, landscape-scale partitioning to prevent such encounters [45, 50, 64, 65]. This suggests they might similarly manage cattle presence without significant long-term displacement. Our study found that while some cheetahs moved away following the cattle playback, most remained stationary or at the playback site throughout the observation period. Therefore, deterrence might be short-lived for the majority. However, the broader implications remain uncertain without data on how far or for how long the deterrent effect lasted among those who moved away from the speaker. To effectively manage cheetah-cattle coexistence, future research should investigate the duration of effects and frequency of interactions. If deterrent effects are brief, cattle presence may pose minimal risks. However, prolonged deterrent effects or frequent interactions could lead to significant disruptions in cheetah movements, habitat use, and reproductive success or survival. Understanding these dynamics will inform strategies to minimize displacement and manage cattle presence in ways that support both livestock production and cheetah conservation.

Our findings that shoats neither deterred nor attracted cheetahs suggest that shoats are unlikely to displace cheetahs or increase predation on them directly. However, we caution that shoats or other livestock, including cattle, can likely produce numerous indirect effects on cheetah presence or livestock predation. High livestock densities can deplete vegetation or disturb habitats, in turn decreasing prey availability for cheetahs [66-68]. This could force cheetahs to move in search of wild prey or force them to attack livestock. In extreme cases, this could lead to local extirpation or a phenomenon called mortality sinks, where individuals are killed in particular areas in response to livestock predation, leaving space for new dispersing individuals, who may also then be killed. Conversely, effective management of livestock grazing could improve habitat quality, attract ungulates, and indirectly benefit cheetahs by increasing prey availability [69-71]. This dynamic could explain why cheetahs have been observed as more likely to stop in areas with moderate livestock grazing [2].

Human activities associated with livestock also present significant indirect effects. Retaliatory actions against cheetahs for real or perceived livestock predation are common, even if predation events are less frequent than other large carnivores [33, 57-59]. Additionally, the presence of domestic dogs, sometimes used to protect livestock [52, 72-76], might influence cheetah movement, although the direct behavioral effects of dogs on cheetah behavior still need to be explored. There may also be potential benefits in areas with lower livestock densities. For example, livestock could flush wild prey, potentially creating hunting opportunities for cheetahs or deter larger carnivores, thereby reducing encounters between cheetahs and their competitors. However, little is known about how other carnivores respond to livestock presence. Measuring how often human herders detect cheetahs or other carnivores in the path of their herds could offer valuable insights into the frequency and nature of these interactions. Such data could provide critical context for understanding how livestock presence influences carnivore behavior beyond direct predation risk. Overall, while further research is required to clarify the complex interactions between cheetahs and livestock, our findings suggest that the effects of shoat presence on cheetahs are likely indirect and context-dependent rather than a simple case of deterrence or attraction.

Limitations: While our methods yielded valuable insights, several limitations warrant consideration. One concern is whether our audio playbacks elicited responses accurately reflecting how cheetahs would naturally behave during interactions with real cattle, shoats, or hornbills. Cheetahs rely heavily on visual cues for detecting threats and prey [43, 49, 50, 63], suggesting the use of visual stimuli instead of audio, might have led to different reactions. However, using live animals for visual cues poses risks to both cheetahs and livestock, and it was not feasible to visually simulate the presence of an entire livestock herd. Therefore, audio playbacks were the safest and most practical method to simulate the presence of livestock and elicit natural responses, an approach supported by numerous studies on wild large carnivores, including cheetahs [20-22, 36-38, 45, 46, 62].

Beyond the limitations of using audio playbacks, our study faced challenges regarding sample size and study conditions. We conducted 32 playback trials on 12 individuals, but the sample size was insufficient for reliably analyzing differences between classes of cheetahs that might respond differently to cattle or shoats. For example, we conducted only eight trials on three males and two trials on a single recently dispersed individual. The larger size of male cheetahs might lead them to perceive our stimuli as less threatening, while recently dispersed cheetahs might approach livestock as easy prey or be extra cautious due to their inexperience. Additionally, direct observations from a vehicle may introduce biases, as the vehicle's presence could influence how cheetahs perceive livestock presence. This is particularly relevant in the Maasai Mara, where herders often avoid stopped vehicles to prevent disturbing tourists from enjoying their cheetah encounters. This could potentially be obvious to cheetahs. Namely, cheetahs might associate livestock presence as less threatening when vehicles are nearby. Lastly, vehicle-based observation limited our trials to specific habitats and daylight hours. Because cheetahs frequently move and hunt at night [77-79], their responses to livestock presence in other contexts could differ. We recommend future research examine whether different groups might respond differently to varying types of livestock presence as this could influence how livestock are managed around certain cheetahs.

*Conservation Recommendations***:** Our findings have implications for managing livestock in areas prioritizing cheetah conservation. Given that cattle may produce short-term deterrent effects, limiting the frequency and duration of these interactions is crucial. However, we found no evidence to recommend prohibiting cattle or shoat grazing if appropriate livestock management practices are in place. Key strategies should include managing livestock density and distribution to limit interactions with cheetahs and minimize indirect effects, such as impacts on habitat suitability and prey availability. Cheetahs tend to avoid cattle, which aligns with findings that they rarely prey on cattle but are more likely to target smaller livestock like calves or shoats. Prioritizing cattle grazing in areas shared with cheetahs may reduce predation risk. However, recognizing that some level of livestock predation by cheetahs will occur, implementing non-lethal strategies, such as defensive livestock herding practices [60, 80], livestock guarding dogs or non-deterrent devices [1, 6, 52, 74, 75, 81], is likely still necessary to mitigate conflicts and promote long-term coexistence.

Methods

Study Site: This study was conducted within four wildlife conservancies on the northern boundary of Kenya’s Maasai Mara National Reserve (MMNR): Naboisho, Olare Motorogi, Ol Kinyei, and Mara North. The MMNR and conservancies share open borders and have minimal permanent human settlements, allowing wildlife to move freely between them and neighboring community areas. Each conservancy is managed independently, with varying degrees of permitted cattle grazing during the day (although illegal grazing occurs in all conservancies, both during the day and at night) [2, 66, 82]. Naboisho and Mara North permit managed cattle grazing year-round, while Olare Motorogi and Ol Kinyei restrict grazing during specific periods, depending on grass abundance and tourism levels. Grazing of shoats is prohibited within all conservancies, but they are frequently observed within the peripheries. Cattle and shoat herds are typically managed separately and accompanied by their young, which may be more susceptible to predation [83, 84]. The conservancies are also renowned for maintaining high densities of many large carnivores, including cheetahs [31], providing an ideal opportunity to observe individuals with previous experience encountering cattle and shoats.

Experimental Procedure: We conducted our audio playback experiment between June 8th and December 20th, 2021. During this time, we exposed individual cheetahs to up to four treatment playbacks, including cattle, shoats, livestock guarding dogs (LGDs), and village dogs (VDs), and two control playbacks we presumed to be neutral, African gray hornbills and Boreal chorus frogs (*Pseudacris maculates*). This paper focused only on the individual responses to the cattle, shoat, and hornbill playbacks, except when evaluating habituation and order effects (Appendices 1 & 2).

Two individuals conducted playback trials: Brian Schuh (B.S.) and Camilla Husted Steinfurth (C.H.S.). Before conducting trials independently, C.H.S. was trained by B.S. on the experimental procedure, which included participation in three actual playback trials. B.S. led C.H.S.'s first trial, providing real-time explanations of the procedure, while C.H.S. conducted her second and third trials under B.S.'s supervision. Throughout the field season, both maintained open communication and addressed any questions or unexpected circumstances before initiating each trial to ensure consistency between trials.

We created three one-minute-long exemplars of each treatment and control playback. Cattle and shoat playbacks were recorded in the Maasai Mara using a Canon 70D camera with an external SMX-20 stereo microphone. To record each playback, we gained permission from livestock owners, asked herders to remain silent, and placed the camera ahead of a moving herd so that it would take at least one minute for heard to reach the camera. We recorded the vocalizations of cattle or shoats and any sounds from bells. During the recording, we also measured the maximum decibels produced by the approaching heard from 40m behind the camera (Appendix 4: Playback Decibels). We trimmed each recording to one minute, concluding the recording when the herd was less than 10 meters from the camera. Hornbill exemplars were sourced from eBird and similarly trimmed to one-minute durations, ensuring that recordings did not start or end abruptly in the middle of a vocalization [91]. We found two African grey hornbills in the field and recorded the maximum decibels they produced from approximately 40m away.

Before conducting trials, all three exemplars of the cattle, shoat, and hornbill playbacks were downloaded onto mobile phones and tested using two first-generation Turtlebox® speakers. For each test, we positioned ourselves 40m away from the speaker. We adjusted the volume level until it matched the decibel levels observed during the recording of that exemplar or the observed decibel levels of wild hornbills (Appendix 4: Playback Decibels). The corresponding volume level for each exemplar was then noted and employed during trials.

To mitigate selection bias, we assigned each known cheetah's playback order and exemplar number before conducting trials with each. When we encountered rare individuals, we assigned the playback order and exemplar number for all six potential trials with that individual in the field before conducting their initial trial. Recognizing the possible challenge of conducting six trials with specific individuals, we randomly assigned one of the control playbacks (i.e., hornbill or frog) to each subject’s first or second trial and the other control playback to their fifth or sixth trial. This ensured that each subject was exposed to treatment and control playbacks within their first two trials. As our subjects have previously encountered cattle, shoats, and VDs, the hornbill playback served as the control playback for these three treatment playbacks. Conversely, the frog playback served as the control playback for the LGD playback as both simulate the presence of novel animals. Therefore, we gave the hornbill playback a 75% chance of being assigned to each subject’s first or second trial and the frog playback a 25% chance. The corresponding treatment playbacks were matched based on the control playback assigned to their first or second trial. For example, if the hornbill playback was randomly assigned to a subject's first trial, the cattle, shoat, and VD playbacks were randomly assigned to their second, third, and fourth trials. The frog and LGD playbacks would be randomly assigned to their fifth and sixth trials. No subject was exposed to the same treatment or control playback twice.

We defined a suitable subject as any solitary cheetah, a randomly selected coalition member, or the mother when cubs were present. The same coalition member was observed for all subsequent trials (up to six). When juveniles separated from their mothers, we randomly selected one of the newly independent cheetahs from the group of siblings to be a new subject. Any playbacks they were exposed to with their mother were excluded from the possible playbacks they could still be exposed to. During one of the initial trials involving a mother cheetah and a very young cub, the mother fled so quickly following the playback that her cub could not keep up. Consequently, we established safety protocols wherein mother cheetahs could not be subjects until independent scientists at the Mara Predator Conservation Programme (MPCP) confirmed her cubs were at least three months old, ensuring cubs could flee with her if necessary. Additionally, if a cheetah was visibly injured (e.g., limping or with an open wound), we postponed trials with that subject until the injury healed, as injured cheetahs might exhibit altered responses (e.g., increased caution), and our playback could potentially have elevated the risk of further injury if the subject were to flee. We resumed trials with injured subjects after an independent evaluation from MPCP confirmed that they no longer displayed apparent behavioral alterations due to injury.

We opportunistically located individuals by searching known home ranges and receiving location reports from conservancy managers, rangers, and tourist guides. While we aimed to balance our search for males and females, females with cubs were more frequently located due to their relatively restricted movement and frequent tracking by tourist guides. At each encounter, individuals were identified by comparing their unique pelage to a database of known individuals maintained by MPCP [28, 85].

After locating a suitable subject, we observed them until specific behavioral and situational criteria were met. These criteria included the subject appearing relaxed, being more than two hours before sunset to allow sufficient time for trial execution, and no disturbances being visible to the observer. We defined ‘relaxed’ as the subject lying down on its side, back, belly, or curled into a circular posture and spending most of its time with its eyes closed. Disturbances were defined as whenever the subject or coalition member was hunting or within 100m of a kill or when large herbivores (i.e., elephants, giraffes, buffalo, or hippo), other vehicles, or other large carnivores (i.e., lions, leopards, hyenas) were visible to the observer. In rare cases, trials were conducted when cattle or shoats were visible from over a kilometer away, provided they were moving away from the subject.

After ensuring the trial criteria were met, we positioned the Bluetooth speaker approximately 40m from the subject (35 – 49m). If any coalition members or cubs were present, we avoided interposing between them and the subject. Since cheetahs in the Maasai Mara are accustomed to tourist vehicles but not people on foot, we quietly opened the door opposite the subject, placed the speaker on the ground, and pointed toward the subject without stepping out of the vehicle. We concealed the speaker behind low rocks or vegetation whenever possible, ensuring it would not obstruct the sound. Following the same guidelines as tourist vehicles observing cheetahs, we maneuvered the observation vehicle to a position approximately 40m away from the subject, aiming for a 45-degree angle between the plane created by the subject and the speaker while ensuring the angle was less than 90 degrees (Figure 1-1). During this process, we observed no apparent behavioral reactions from any subjects.

To initiate a trial, we switched off the vehicle’s engine and started recording the subject with a video camera. B.S. used a Samsung Galaxy S21 Ultra, while C.H.S. used a Sony HDR-PJ780VE Handycam. We quietly spoke the date, the subject’s name, which playback and exemplar the subject would be exposed to during that trial, and the direction (left/right) and distance the speaker was placed from the subject. Finally, we spoke the exact time to start a five-minute initial observation period (IOP). The trial was terminated if any disturbance (defined above) occurred during the IOP. The disturbance was verbally noted if this happened, and we stopped video recording. Once the criteria for a trial were met again, we started recording a new trial video and IOP.

At the end of the IOP, we played the assigned playback for that subject and trial. We continued to video-record the subject throughout the post-playback period (PPP) until the trial ended for one of the following reasons: a) The subject disappeared from the observer's view because they moved and settled in thick brush or fled the trial location. b) Other vehicles or domestic animals approached within 200m of the subject. This distance was determined based on our ability to detect vehicles and domestic animals from 100m away, reducing the chances of subjects reacting to actual disturbances before we ended the trial. c) The maximum PPP duration of one hour was met, resulting in a total observation time of 1 hour and 5 minutes, including the IOP. Upon a trial's conclusion, the reason for ending the trial was quietly spoken before we stopped video recording.

We implemented a one-week washout period between trials for individuals to minimize potential carryover effects. This allowed the subjects to encounter livestock and other-human-associated stimuli before exposure to another playback, reducing the possibility of habituation and restoring salience.

Coding Videos: The subject's behavior in each trial video was coded by three individuals using BORIS®. Before coding actual trial videos, all three individuals discussed how to record each behavior (defined below) using a five-minute training video featuring a cheetah from the Maasai Mara. Following this discussion, each person independently coded an additional five-minute training video to ensure a consistent understanding of the behavioral definitions. Each training video depicted a cheetah displaying behaviors similar to those measured in actual trial videos.

To mitigate measurement bias, all trial videos were coded blindly to the playback (i.e., cattle, shoat, hornbill) and were watched without sound. Individuals conducting specific trials also did not code the respective trial videos. We aimed to code each trial video in a single session, covering the IOP and PPP.

To evaluate intercoder reliability, three trial videos assigned to each coder were independently coded by another person, resulting in nine trial videos being coded by two individuals. We compared how each coder measured vigilance toward the speaker and activity (defined below) for these videos. Measurement precision was assessed by calculating the average absolute difference between corresponding behavioral measures recorded by the two individuals across all nine videos. Our findings indicate an average measurement precision of 0.1% for activity and 1.5% for vigilance (Appendix 3: Intercoder Reliability – Table 1-A3-1).

Measuring Behaviors: We measured five behavioral responses during each trial video: latency to initiate movement (latency), time spent moving toward the speaker, time spent moving away from the speaker, time spent active, and time spent vigilant toward the speaker. We defined latency as the time (min:sec) between playback initiation and the subject's first movement.

We measured time spent moving toward and away from the speaker only after playback initiation, throughout the entire PPP (≤1 hour), as our behavioral criteria for conducting a trial restricted movement during the IOP. We defined movement toward the speaker as any movement within an arc of less than 90° relative to the plane formed by the camera, subject, and the left or right edge of the video frame, depending on the direction of the speaker's placement (gray arc, Figure 1-1). Movement away from the speaker included movement in all other directions (white area, Figure 1-1). We did not measure speed or distance traveled.

We recorded time spent active and vigilant toward the speaker across the entire trial video (IOP + PPP). At the start of each trial, we required subjects to be relaxed (defined above). We defined a subject as active if it changed body posture or moved, including sitting, standing, or walking, as these shifts often indicate changes in behavioral intention [20, 21, 24, 46, 62, 86-88]. We did not measure the direction of activity. In rare cases where obstacles obscured our view of the subject's body, we recorded activity as 'unknown' until visibility was restored.

Vigilance toward the speaker was measured by adapting the approach by Durant (2000), who measured cheetah vigilance toward lion and hyena playbacks [45]. We recorded a subject as vigilant if it directed its gaze beyond its body, associates, or immediate surroundings within the same <90° arc we used for movement toward the speaker (gray arc, Figure 1-1). This consistent measurement angle accounted for variability in speaker placement relative to the camera and allowed us to reliably observe the subject's eyes, aiding in our ability to confirm instances of vigilance when their gaze was directed toward the speaker. This approach minimized uncertainties in identifying vigilance, particularly when subjects directed their gaze away from the camera, making observing their eyes impossible. We did not record vigilance if the subject's eyes were closed or directed outside of the defined arc (white area, Figure

1-1). In rare cases when obstacles obscured the observer's view of the subject’s eyes while directing their gaze toward the speaker, we recorded vigilance as ‘unknown’ until visibility was restored.

Response Variables: From our five behavioral measures, we calculated three response variables for each subject and trial: movement response score, change in percent time active, and change in percent time vigilant toward the speaker.

We calculated the movement response score by subtracting the time the subject spent moving away from the speaker from their time spent moving toward it (net percent time moving toward or away from the speaker), then dividing this value by their latency to move. A greater negative score indicates faster, prolonged movement away from the speaker, suggesting *Deterrence*, while a greater positive score indicates faster, prolonged movement toward the speaker, suggesting *Attraction*. Individuals that did not move received a movement response score of zero.

We acknowledge that dividing net percent time moving by other factors, such as PPP duration instead of latency, would also provide insights into individual responses. However, we selected latency due to its conservative nature and its use in prior studies [45] . Using PPP duration might skew response intensity if trials ended early due to external factors (e.g., approaching vehicles), potentially exaggerating movement effects. Conversely, latency may underestimate response intensity if subjects remained stationary and their trials ended early, eliminating the possibility of us observing movement due to our playback. This conservative measure makes it less likely to find a false effect.

We calculated changes in percent time active and vigilant toward the speaker across two timescales: the entire PPP and consecutive five-minute post-playback intervals (PPIs; PPI 1 = 0 – 5 min post-playback, PPI 2 = 5 – 10 min, etc.). The five-minute interval duration mirrors that of the IOP, providing a direct comparison and allowing us to analyze how individuals exhibited each behavior over time. We calculated changes by subtracting each behavior's duration during the IOP from the PPP or each PPI. For individual PPIs, we required a minimum observation of 30 seconds. For example, if a PPP lasted 10:20 min:sec, we analyzed behavioral changes throughout the entire PPP, and during PPI 1 and 2, but omitted PPI 3 due to its shorter duration.

Analysis

Statical Significance: We applied Bonferroni correction to account for multiple comparisons, with a p-value of 0.05 – 0.01 considered suggestive and $p < 0.01$ considered significant [39, 89, 90].

Movement: We used both within-cheetah and between-cheetah analyses to test for *Deterrence* or *Attraction*. We began with one-sample Wilcoxon signed rank tests for within-cheetah tests to determine if median movement response scores differed significantly from zero after cattle, shoat, or hornbill playbacks (Table 1-1). We then applied a modified Hills-Armitage approach to compare movement scores across playback conditions (cattle vs. hornbill, shoat vs. hornbill, cattle vs. shoat) [40]. In this approach, we grouped individuals exposed to each playback pair based on the sequence in which they were exposed to each (e.g., cattle first and hornbill second, hornbill first and cattle second), calculated the difference in movement response scores between the playbacks, and used two-sample Wilcoxon rank sum tests to compare the median difference between groups (Table 1-1). Due to logistical constraints, some within-cheetah tests had reduced sample sizes as not all cheetahs were exposed to each playback pair. For between-cheetah tests, we used Wilcoxon rank sum tests to compare median movement response scores between all cheetahs exposed to each playback in each comparison (Table 1-1).

Vigilance & Activity: We used both within-cheetah and between-cheetah analyses to examine changes in activity and vigilance toward the speaker following cattle, shoat, and hornbill playbacks. For within-cheetah tests, we began with two-sample Wilcoxon signed-rank tests to determine if the median percent time spent active and vigilant during PPI 1 and the entire PPP differed from the median percent time during the IOP of the same trial. To compare changes in activity and vigilance between playbacks, we calculated the change in each behavior across both timescales (PPI 1 and PPP) by subtracting the percent time each behavior was exhibited during the IOP from the percent time exhibited during PPI 1 and PPP. We then applied the modified Hills-Armitage approach (described above) and Wilcoxon rank sum tests to compare the median changes across playback conditions (cattle vs. hornbill, shoat vs. hornbill, cattle vs. shoat) [40]. Due to logistical constraints, some within-cheetah tests had reduced sample sizes when individuals were not exposed to each playback pair. For between-cheetah tests, we used

Wilcoxon rank sum tests to compare median changes in activity and vigilance between all cheetahs exposed to each playback in each comparison. If statistically significant changes in either behavior were found during PPI 1, we applied the same analysis methods to subsequent PPIs until no further differences were detected.

Habituation: We evaluated habituation by testing whether individuals exposed to three or more playbacks (n = 9; six total playbacks, including cattle, shoat, and hornbill) exhibited decreasing changes in activity or vigilance toward the speaker during PPI 1 and or the entire PPP of each trial as they were exposed to more playbacks. Individuals exposed to three or fewer playbacks (n = 3) were excluded due to the increasing likelihood of habituation with greater exposure. To encompass the potential habituation to our method (e.g., speaker placement), we considered the total number of playbacks (including treatment and control playbacks) rather than just the treatment playbacks. We used Spearman's rank correlation rho tests to initially examine whether individual changes in either behavior during PPI 1 or the entire PPP decreased with increased exposure to more playbacks (Appendix 1: Habituation – Table 1-A1-1). Subsequently, we used one-sample Wilcoxon signed rank tests to determine whether the slope parameters for each behavior change during the two timescales statistically differed from zero, with negative slope parameters indicating reduced changes in behavior as individuals were exposed to more playbacks (Appendix 1: Habituation – Table 1-A1-2).

Order Effect: We assessed whether the sequence of playback exposure influenced cheetah responses using a modified Hills-Armitage approach [40]. For within-cheetah tests of each treatment stimulus (LGD, VD), we categorized individuals into Treatment-First and Control-First groups based on the initial stimulus they encountered (treatment or control). While some cheetahs were exposed to other stimuli between these playbacks, our randomized stimuli sequence and habituation assessment increased our confidence that intermediate exposures had minimal influence on responses. We calculated the difference in activity and vigilance change for each individual during PPI 1 and the entire PPP following exposure to treatment and control stimuli (treatment – control). We then used a two-sample Wilcoxon rank sum test to compare median differences in behavior change between Treatment-First and Control-

First groups (Appendix 2: Order-Effect – Table 1-A2-1). Any statistical difference in behavior change during any period suggests potential within-subject order effects for that treatment stimulus.

For grouped assessments, cheetahs exposed to each treatment stimulus were divided into two groups based on whether they encountered the stimulus during their first three or last three trials. We then compared the median change in activity and vigilance between these two groups for each treatment stimulus during PPI 1 and the entire PPP (Appendix 2: Order-Effect – Table 1-A2-2). We infer any statistical differences as potential grouped order effects for that treatment stimulus.

Appendix 1: Habituation

We evaluated habituation by testing whether individuals exposed to three or more playbacks (n = 9; six total playbacks, including LGD, VD, and frog playbacks) exhibited decreasing changes in vigilance toward the speaker and activity during PPI 1 and or the entire PPP of each trial as they were exposed to more playbacks. Individuals exposed to three or fewer playbacks (n = 3) were excluded due to the increasing likelihood of habituation with greater exposure. To encompass the potential habituation to our methodology (e.g., speaker placement), we considered the total number of playbacks (including treatment and control playbacks) rather than just the treatment playbacks. We used Spearman's rank correlation rho tests to initially examine whether individual changes in either behavior during PPI 1 or the entire PPP decreased with increased exposure to more playbacks (Table 1-A1-1). Subsequently, we used one-sample Wilcoxon signed rank tests to determine whether the slope parameters for each behavior change during the two timescales statistically differed from zero, with negative slope parameters indicating reduced changes in behavior as individuals were exposed to more playbacks (Table 1-A1-2). We found no evidence of habituation.

Table 1-A1-1: Changes in vigilance and activity for individual cheetahs as they were exposed to increasing number of playbacks.

Cheetah Name/Interval & Behavior Change	**1st Post-Playback Interval**						**Post-Playback Period**					
	Change in Vigilance			Change in Activity			Change in Vigilance			Post-Playback Period		
	rho =	S =	p =	rho =	S =	p =	**rho =**	**S =**	**p =**	**rho =**	**S =**	**p =**
Entito (n = 6)	-0.14	40	0.8	-0.13	39.58	0.8	-0.61	56.31	0.2	-0.52	53.26	0.23
Kuahidi (n = 6)	-0.37	48	0.5	-0.17	40.92	0.75	-0.03	36	1	-0.06	37.03	0.91
Kulete (n = 6)	0.43	20	0.42	-0.64	57.32	0.17	0.77	16	0.78	-0.71	60	0.14
Nebaati (n = 6)	0.6	14	0.24	0.21	27.56	0.69	-0.14	40	0.8	0.31	24	0.56
Mbili (n = 6)	0.03	33.99	0.96	-0.64	57.31	0.17	-0.03	36	1	-0.64	57.31	0.17
Neema (n = 5)	0.3	14	0.68	0.7	6	0.69	-0.3	26	0.68	-0.9	38	0.08
Selenkei (n = 5)	0.3	14	0.68	0.11	17.76	0.86	0.41	11.79	0.49	0.2	16	0.78
Sila (n = 5)	0.3	14	0.68	-0.1	22.1	0.87	0.3	14	0.68	-0.3	26	0.68
Leteipa (n = 5)	0.6	8	0.35	0.67	6.58	0.22	0.2	16	0.78	0.67	6.58	0.22

Correlations were tested with Spearman's rank correlation rho tests.
n refers to the number of playbacks each individual was exposed to.

Table 1-A1-2: Habituation test examining whether the slope parameters of individual cheetahs differ from zero.

Interval & Behavior Change	**Median rho =**	**V =**	**p =**
1st Post-Playback Interval			
Change in Vigilance	0.3	37	0.1
Change in Activity	-0.1	24	0.91
Post-Playback Period			
Change in Vigilance	-0.03	25.5	0.77
Change in Activity	-0.3	13	0.3

Comparison was completed with the Wilcoxon signed rank test.
Median rho value was calculated from the slope parameters calculated for individual cheetahs in Appendix 1: Habituation - Table 1-A1-1.

Appendix 2: Order-Effect

Within-Subject Tests: For within-subject assessments of each treatment stimulus (cattle, shoat), individuals exposed to both treatment and control stimuli (hornbill) were divided into Treatment-First and Control-First groups based on which stimulus they were exposed to first, following the Hills-Armitage approach. While some cheetahs were exposed to other stimuli between the two stimuli, we hope our random sequence of stimuli and assessment of habituation raise confidence that intermediate exposures had minimal influence on responses. For each individual, we calculated the difference in change in vigilance toward the speaker and activity during PPI 1 and the entire PPP following exposure to the treatment and control stimuli (treatment – control). We then used a two-sample Wilcoxon rank sum test to compare the difference in median change for both behaviors between Treatment-First and Control-First individuals (Table 1-A2-1). We found no statistical difference in either behavior during any period, suggesting no order effect (Table 1-A2-1).

Table 1-A2-1: Within-subject subject tests comparing median changes in percent time active and vigilant toward the speaker among individual cheetahs who received a treatment playback before the control and individuals who received the control playback before treatment, and between individuals who received the cattle playback before the shoat and individuals who received the shoat playback before the cattle.

Cattle vs. Hornbill	Cattle-First (n = 5)	Hornbill-First (n = 5)	W =	p =
Vigilance Toward the Speaker	Median Difference (IQR)	Median Difference (IQR)		
1st Post-Playback Interval	17% (16% to 47%)	24% (15% to 27%)	15	0.69
Post-Playback Period	15% (13% to 23%)	5% (-4% to 20%)	17	0.42
Change in Activity	Median Difference (IQR)	Median Difference (IQR)		
1st Post-Playback Interval	10% (0% to 52%)	0% (0% to 2%)	15.5	0.59
Post-Playback Period	2% (0% to 16%)	2% (-1% to 2%)	15	0.68
Shoat vs. Hornbill	Shoat-First (n = 3)	Hornbill-First (n = 7)	W =	p =
Vigilance Toward the Speaker	Median Difference (IQR)	Median Difference (IQR)		
1st Post-Playback Interval	14% (-7% to 17%)	40% (36% to 56%)	2	0.07
Post-Playback Period	-1% (-14% to 0%)	5% (16% to 47%)	3	0.12
Change in Activity	Median Difference (IQR)	Median Difference (IQR)		
1st Post-Playback Interval	75% (38% to 77%)	2% (0% 62%)	11.5	0.91
Post-Playback Period	18% (9% to 52%)	4% (-2% to 34%)	13.5	0.57
Cattle vs. Shoat	Cattle-First (n = 4)	Shoat-First (n = 5)	W =	p =
Vigilance Toward the Speaker	Median Difference (IQR)	Median Difference (IQR)		
1st Post-Playback Interval	4% (-16% to 7%)	13% (-5% to 34%)	9.5	0.6
Post-Playback Period	-8% (-25% to 10%)	16% (12% to 20%)	5	0.29
Change in Activity	Median Difference (IQR)	Median Difference (IQR)		
1st Post-Playback Interval	-10% (-39% to 78%)	-13% (-32% to 0%)	8	0.42
Post-Playback Period	-2% (-14% to 16%)	-2% (-34% to	7	0.56

Comparisons were analyzed using the Hills-Armitage approach [40] and Wilcoxon rank sum test. Individuals receiving only one playback were excluded.
Between-subject comparisons were analyzed using the Wilcoxon rank sum test.
IQR refers to Inter Quartile Range of the Median difference.

Between-Subject Tests: For grouped assessments, cheetahs exposed to each treatment stimulus were divided into two groups based on whether they encountered the stimulus during their first three or last three trials. We then compared the median change in vigilance and activity between these two groups for each treatment stimulus during PPI 1 and the entire PPP. We found no statistical differences, suggesting no order effect (Table 1-A2-2).

Table 1-A2-2: Between-subject subject tests comparing median changes in percent time active and vigilant toward the speaker among individual cheetahs who were exposed to the cattle and shoat playbacks during trial 1 - 3 and those who were exposed to them during trials 4 – 6.

Cattle vs. Hornbill	**Cattle Exposure, Trials 1 - 3 (n = 6)**	**Cattle Exposure, Trial 3- 4 (n = 4)**	**W =**	**p =**
Vigilance Toward the Speaker	Median Difference (IQR)	Median Difference (IQR)		
1st Post-Playback Interval	33% (18% to 47%)	40% (27% to 52%)	8	0.48
Post-Playback Period	26% (0% to 44%)	15% (0% to 17%)	13	0.91
Change in Activity	Median Difference (IQR)	Median Difference (IQR)		
1st Post-Playback Interval	40% (7% to 60%)	0% (0% to 13%)	3	0.12
Post-Playback Period	52% (13% to 57%)	6% (2% to 11%)	17	0.33
Shoat vs. Hornbill	**Shoat Exposure, Trials 1 - 3 (n = 7)**	**Shoat Exposure, Trial 3- 4 (n = 3)**	**W =**	**p =**
Vigilance Toward the Speaker	Median Difference (IQR)	Median Difference (IQR)		
1st Post-Playback Interval	23% (13% to 38%)	50% (47% to 54%)	17	0.31
Post-Playback Period	4% (-1% to 7%)	12% (12% to 34%)	2	0.07
Change in Activity	Median Difference (IQR)	Median Difference (IQR)		
1st Post-Playback Interval	39% (0% to 69%)	83% (41% to 87%)	5.5	0.29
Post-Playback Period	18% (4% to 45%)	29% (15% to 36%)	11.5	0.91

Between-subject comparisons were analyzed using the Wilcoxon rank sum test.
IQR refers to the Interquartile Range of Median Difference.

Appendix 3: Intercoder Reliability

We evaluated intercoder reliability across nine actual trial videos. Each coder, Brian Schuh (B.S.), Camilla Husted Steinfurth (C.H.S.), and Kim Preston (K.P.), independently coded three trial videos assigned to each of the other coders. We compared how each coder measured activity and vigilance toward the speaker. Measurement precision was assessed by calculating the average absolute difference between corresponding behavioral measures recorded by the two individuals across all nine videos. Our findings indicate an average measurement precision of 0.1% for activity and 1.5% for vigilance toward the speaker (Table 1-A3-1).

Table 1-A3-1: Intercoder reliability tests across nine actual trial videos.

Interobserver Reliability Test				
	B.S.	**C.H.S.**	**K.P.**	**Measurement Precision**
Video 1 (1:05:00 hr:min:sec)				
Vigilant Toward Speaker	17.9%	18.2%		0.3%
Active	3.5%	3.4%		0.1%
Video 2 (1:05:00, hr:min)				
Vigilant Toward Speaker	27.7%	25.6%		2.1%
Active	3.3%	3.3%		0.0%
Video 3 (1:05:00, hr:min:sec)				
Vigilant Toward Speaker	10.3%	10.2%		0.1%
Active	1.6%	1.6%		0.0%
Video 4 (0:12:48, hr:min:sec)				
Vigilant Toward Speaker	24.3%		24.5%	0.2%
Active	59.6%		59.9%	0.3%
Video 5 (1:05:00, hr:min:sec)				
Vigilant Toward Speaker	19.6%		18.3%	1.3%
Active	0.0%		0.0%	0.0%
Video 6 (0:49:08, hr:min:sec)				
Vigilant Toward Speaker	10.2%		12.7%	2.5%
Active	0.0%		0.0%	0.0%
Video 7 (0:22:15, hr:min:sec)				

Vigilant Toward Speaker		16.0%	16.2%	0.2%
Active		17.9%	17.6%	0.3%
Video 8 (0:43:28, hr:min:sec)				
Vigilant Toward Speaker		22.1%	20.7%	1.4%
Active		0.0%	0.0%	0.0%
Video 9 (1:05:00, hr:min:sec)				
Vigilant Toward Speaker		23.5%	28.6%	5.1%
Active		0.8%	0.8%	0.0%
Average Measurement Precision - Vigilant Toward Speaker				1.5%
Average Measurement Precision - Active				0.1%

B.S. indicates coder Brian Schuh
C.H.S. indicates coder Camilla Husted Steinfurth
K.P. indicates coder Kim Preston

Appendix 4: Playback Decibels

Table 1-A4-1: Observed and achieved playback decibels.

Playback	Observed (dB)	Exemplar #	Achieved (dB)
Cattle	68	1	67.1
		2	60.3
		3	63.6
Shoat	44.8	1	45.6
		2	43.7
		3	45.2
Hornbill	54	1	55.3
		2	53.7
		3	52.9

Observed decibels were recorded from 40m of a cattle and shoat herd, or from wild hornbills. Achieved decibels were measured from 40m away from the playback speaker.

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Chapter 2: Experimental Evaluation of the Behavioral Responses of Cheetahs to Vocalizations from Livestock Guarding Dog and Non-Livestock Guarding Dog Breeds

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Abstract. Human-carnivore conflict remains a significant conservation challenge, particularly in areas where carnivores encounter humans and their domestic animals. Specialized breeds of domestic dogs, known as livestock guarding dogs (LGDs), are widely used and promoted as a non-lethal method for protecting livestock by deterring carnivores. In addition, other non-LGD breeds (referred to here as village dogs, VDs) often accompany humans or roam freely in shared landscapes, potentially influencing carnivore behavior by acting as either threatening competitors or prey. However, the direct effectiveness of LGDs in deterring individual carnivores remains poorly understood. Furthermore, carnivore responses to different dog breeds have never been directly compared, leaving uncertainty about whether specific breeds are more likely to deter or attract individuals. Here, we experimentally tested the short-term behavioral responses of wild cheetahs (*Acinonyx jubatus*) to audio playbacks of LGD and VD vocalizations, as well as two control species (frogs and hornbills), during randomized crossover trials. We tested contrasting hypotheses for each breed: *Deterrence*, predicting movement away from the playback speaker, and *Attraction*, predicting movement toward it. Our findings show that LGDs elicited movement away from the speaker in five of eleven cheetahs, providing limited support for Deterrence. In contrast, VDs elicited movement in only two of nine cheetahs, with one moving toward and one moving away from the speaker, providing equivocal evidence for hypotheses. These results support the use of LGDs as a tool to protect livestock, as their presence can deter some cheetahs. However, variability in individual responses suggests that reduced livestock losses associated with LGDs may also result from alerting humans, who can then intervene. Furthermore, the observed deterrence highlights the need for future research on the duration and severity of LGD-induced displacement to assess potential long-term impacts on cheetahs. In contrast, VDs appear to minimally impact cheetah behavior, providing the first evidence

that individuals may respond differently to the vocalizations of distinct dog breeds. Nonetheless, the potential indirect effects of VDs, such as competition for prey or disease transmission, underscore the importance of regulating their densities or behaviors to minimize negative impacts and promote coexistence in shared landscapes.

Introduction

Humans and their domestic animals frequently occupy areas within large carnivore habitats. In response, individual carnivores often adjust their spatiotemporal patterns of movement over hours to days to avoid these areas, move through them more quickly, or use them when encounters with humans or domestic animals are less likely [1-7]. Nevertheless, interactions between humans and carnivores still occur [8-10]. In such cases, carnivores may threaten people or domestic animals [11-20], whereas people may threaten carnivores [10, 21-25]. This ultimately threatens carnivore populations [10, 21-25]. In response, numerous studies have focused on promoting coexistence by developing interventions that mitigate conflict, such as legally protecting carnivores, regulating human and domestic animal presence, and implementing non-lethal methods to deter carnivores from livestock [17, 23, 26-30]. However, a critical gap remains in our understanding of individual carnivores' short-term (seconds to hours) behavioral reactions in the lead-up to encounters. Gaining such knowledge could help explain why conflicts occur and lead to more effective strategies for reducing conflict and improving coexistence.

Our limited understanding of short-term carnivore responses to humans and domestic animals is primarily due to the challenges associated with directly observing interactions between individual carnivores and experimentally manipulated human-associated stimuli. Carnivores often persist at low densities and avoid detection by people, making locating and observing the same individual difficult over time. Furthermore, controlling when and where carnivores interact with specific stimuli is often infeasible in wild settings. As a result, we have little generalized theory to predict the outcomes of varied, individual interactions between people, domestic animals, and wild carnivores. People, therefore, rely on untested assumptions about whether all carnivores are problematic individuals or whether all are deterred or attracted to humans, domestic animals, or other property. For example, assuming a carnivore that once attacked a domestic animal will do so again could erroneously promote only lethal intervention to prevent future attacks. Conversely, assuming a carnivore that was scared away by humans or domestic animals during a single encounter could erroneously lead to habituated carnivores. Therefore, understanding individual variations in carnivore reactions to humans and domestic animals could shed light on human-carnivore interactions in many areas where both coexist.

Dogs are among the most common domestic animals in carnivore habitats, often found on the peripheries of urban landscapes, around rural homes, accompanying humans during recreational activities, guarding livestock, or roaming freely as feral individuals or in packs [31-35]. During interactions, carnivores may be deterred or attracted to dogs. For example, livestock owners who use specialized breeds of dogs, known as livestock guarding dogs (LGDs), report fewer livestock losses to carnivores, with indirect evidence from experimental tests corroborating these perceptions [28, 29, 36-42]. This implies that the presence of dogs might deter carnivores. Conversely, numerous studies document carnivores killing and consuming dogs as prey [43, 44], suggesting they may attract some carnivores. One factor that may explain these opposing responses is the breed of dog. LGDs, such as Anatolian shepherds, are often assumed to deter carnivores more effectively than non-LGD breeds due to their larger size, deeper barks, or instinct to bond with and protect livestock. In contrast, non-LGD breeds, especially smaller ones, are often presumed to be less threatening and more likely to present opportunities for predation. However, scant evidence exists to predict whether individual carnivore responses align with these assumptions. For example, while LGDs may reduce livestock predation by directly deterring carnivores, they may also do so indirectly by alerting nearby humans who intervene when a carnivore approaches.

Only a few studies have directly observed carnivore-dog interactions, providing limited and mixed evidence for deterrence or attraction. Two used night vision cameras to observe wolves both avoiding and approaching sheep in the presence of LGDs [45, 46], while another employed motion cameras and audio playbacks of barks from non-LGD breeds at puma feeding sites, finding little reaction from the pumas [47]. Both studies, however, had key limitations. The former two observed wolves only after they had already approached livestock herds, missing opportunities to observe how wolves might react in other situations, such as when LGDs approach them, where deterrence might be more likely. The latter focused exclusively on puma reactions at feeding sites, where pumas may exhibit altered behavior, such as being less likely to be deterred while defending their kill. Although insightful, the previous studies leave unanswered questions about how dog breeds influence carnivore behavior and how individual carnivore reactions may vary to the same dog stimuli. Understanding how carnivores respond to dogs requires direct observations of experimentally manipulated encounters.

Here, we directly observe and compare the short-term reactions of individual cheetahs (*Acinonyx jubatus*) to audio playbacks of vocalizations from two dog breeds, LGDs (Anatolian shepherds) and a mixed-breed we refer to as village dogs (VDs), alongside two neutral control animals (hornbills and frogs), in four randomized crossover trials. We experimented in four wildlife conservancies surrounding Kenya's Maasai Mara National Reserve, which has a high density of individually identifiable cheetahs habituated to human observation from vehicles [48]. The VD playback, recorded locally in the Maasai Mara, simulated the presence of dogs our subjects have likely encountered. In contrast, the LGD playback was novel to our subjects. By incorporating vocalizations from native hornbills and non-native frogs as control stimuli, we assessed whether individual responses to the LGD playback reflected novelty alone. We test contrasting hypotheses for both dog breeds: *Deterrence*, predicting that cheetahs will move away from the dog playback, and *Attraction*, predicting that cheetahs will move toward it (Figure 2-1). Although limited knowledge exists about how cheetahs respond to domestic dogs, we expect individuals will be deterred, particularly by LGDs, which are widely promoted as a method to protect livestock from cheetahs [28, 37-39, 49, 50]. This prediction is based partly on the subordinate status of cheetahs relative to more dominant large carnivores [51-56]. However, our research design also accounts for *Attraction* and enables within-subject comparisons to assess inter-individual variation in responses to different dog breeds versus control playbacks.

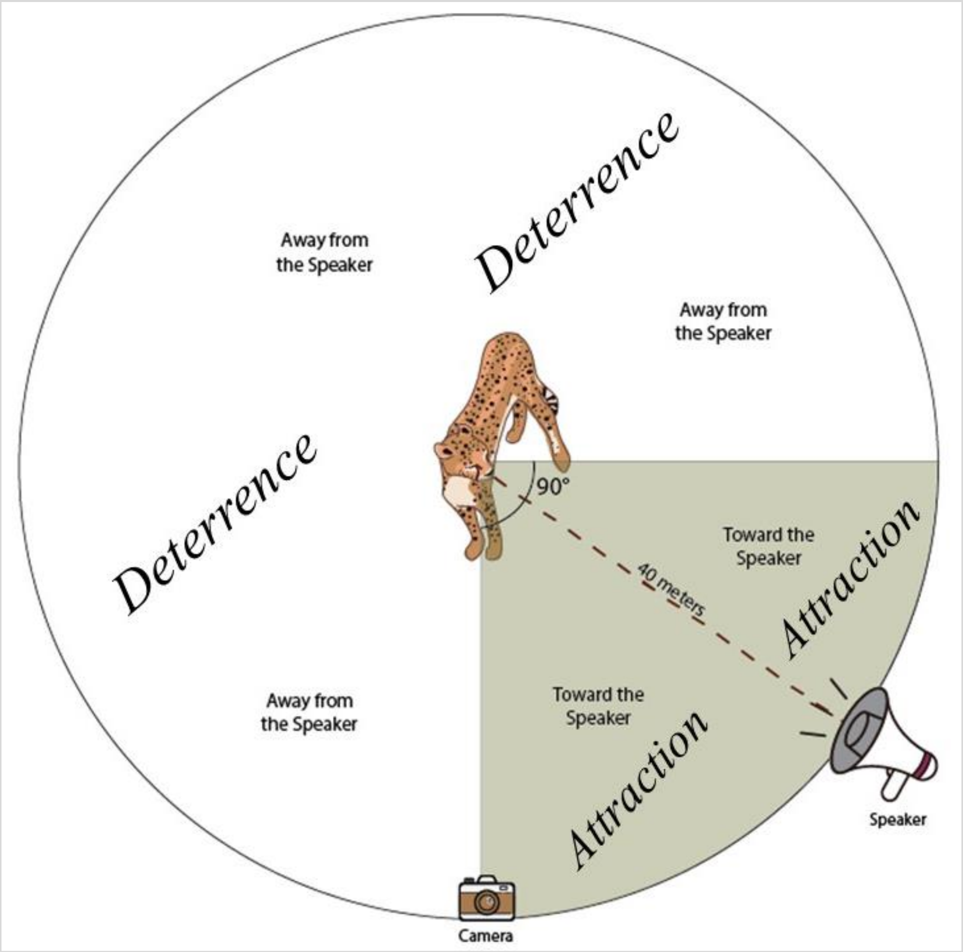

Figure 2-1: *Deterrence* is supported if individuals move away from the speaker following either dog playback. *Attractive* is supported if individuals move toward the speaker following either dog playback. A subject moved toward the speaker when it moved within the gray arc (< 90° arc from the camera to the speaker and directly left or right of the subject). A subject moved away from the speaker when it moved in any other direction (white area). We measured individuals' time spent vigilant when it visually scanned toward the speaker (gray arc). We did not measure time spent vigilant (scanning) in any other direction (white area).

To differentiate *Deterrence* from *Attraction*, we measured two movement response variables for each cheetah following each audio playback: the time from playback initiation to the first movement (latency to move) and the net percent time spent moving away from or toward the playback speaker (Figure 2-1). We separately compared responses to playbacks simulating familiar animals (VDs and hornbills) and novel animals (LGDs and frogs). *Deterrence* would be supported if individuals exhibited significantly more movement away from the speaker, while *Attraction* would be supported if individuals exhibited significantly more movement toward the speaker [57-59]. The null hypothesis would be supported if movement in response to either dog playback matched reactions to the respective control or if individuals did not move in response to either dog playback [47].

We assess the salience of each playback (i.e., its significance to the cheetahs) by measuring individual changes in percent time active and vigilant toward the speaker (Figure 2-1) before and after each. Activity changes include adjustments in body posture, such as sitting, standing, or any movement (i.e., whenever the subject is not lying down). This broad definition of activity enables us to capture behaviors that may indicate an intention to move, even for individuals that remain stationary. Meanwhile, changes in vigilance toward the playback speaker reflect heightened attention to the stimulus [60]. Although changes in activity and vigilance may not distinguish between *Deterrence* and *Attraction*, they provide insight into the meaningfulness of the playbacks. A strength of our randomized crossover trial design is the within-subject comparisons, which control for inter-individual variability and reduce common errors associated with wildlife research [61]. Between-subject comparisons further reveal inter-individual differences in response to the same stimuli.

If *Deterrence* were supported, we might recommend using dogs for livestock protection, depending on the severity of deterrence observed. However, this may also risk long-term cheetah displacement, suggesting a need to limit dog density, restrict their distribution, or even prohibit dogs in areas critical for cheetah conservation. Conversely, if Attraction is supported for either breed, increased encounters and conflicts between cheetahs, domestic dogs, and people might be expected. Cheetahs could prey on dogs or livestock, while dogs or people might harm cheetahs preemptively or in retaliation. These dynamics could create mortality sinks, where domestic dogs attract cheetahs to territories with higher mortality risks. Thus, our hypotheses have important implications for adapting interventions to address interactions between cheetahs, dogs, and people within shared landscapes.

Methods

Study Site. This study was conducted in four wildlife conservancies on the northern boundary of Kenya’s Maasai Mara National Reserve (MMNR): Naboisho, Olare Motorogi, Ol Kinyei, and Mara North. The MMNR, conservancies, and surrounding community areas share open borders, allowing wildlife to move freely between each. Despite being prohibited, village dogs (VDs) commonly roam freely into conservancies or enter with residents and livestock [34], increasing the likelihood of interactions with cheetahs. Specialized livestock guarding dogs (LGD) breeds are absent in the conservancies and community areas.

Experimental Procedure. We conducted our audio playback experiment between June 8th and December 20th, 2021. We exposed individual cheetahs to up to four treatment playbacks, including LGDs, VDs, cattle (Described in Chapter 1), and shoats (Described in Chapter 1), and two control playbacks we presumed to be neutral, African gray hornbills (*Lophoceros nasutus)* and Boreal chorus frogs (*Pseudacris maculates*). This chapter focuses only on individual responses to the LGD, VD, hornbill, and frog playbacks, except when evaluating habituation (Appendix 1: Habituation).

Two individuals conducted playback trials: Brian Schuh (B.S.) and Camilla Husted Steinfurth (C.H.S.). Before conducting trials independently, C.H.S. was trained by B.S. on the experimental procedure, which included participation in three actual playback trials. B.S. led C.H.S.'s first trial, providing real-time explanations of the procedure, while C.H.S. conducted her second and third trials under B.S.'s supervision. Throughout the field season, both maintained open communication and discussed any questions or unexpected circumstances before initiating each trial to ensure consistency.

We created three one-minute exemplars of each treatment and control playback. LGD exemplars were created from audio recordings of Anatolian shepherds provided by Calum O'Flaherty at the Cheetah Conservation Fund (CCF) in Namibia. The recordings captured multiple LGDs barking from less than 10m away, and the maximum decibel levels were measured from 40m away (Appendix 4: Playback Decibels), mirroring the intended distance we aimed to place the speaker from the subject during a trial. VD exemplars were created from video recordings of VDs recorded by B.S. in the Maasai Mara. These recordings captured multiple VDs barking from less than 10m away and were later converted to audio files using Audacity®. After recording VD barks, we measured the maximum decibels the same dogs produced from 40m away (Appendix 4: Playback Decibels). We trimmed each LGD and VD recording into three one-minute mp3 files, each with unique barks, ensuring none started or ended in the middle of a bark. Fences and other background anthropogenic noises could be heard in some recordings between barks. To remove these noises, we recorded the natural ambient background noise at our camp in the Maasai Mara. We replaced the periods between dog barks in each LGD and VD exemplar with a section of this recording. We ensured the same amount of time between dog barks and that no other anthropogenic noises were included in the exemplars. We then tested each exemplar to ensure the moments when the two recordings were spliced together were not noticeable by asking multiple people who never heard the original recordings.

Hornbill exemplars were sourced from eBird and similarly trimmed to one-minute durations, ensuring each did not start or end in the middle of a vocalization [101]. We found two African grey hornbills in the field and measured the maximum decibels they produced from approximately 40m away (Appendix 4: Playback Decibels).

We recorded each frog exemplar on audio and video in Winnebago County, Illinois, using a Samsung Galaxy S21 Ultra from less than 10m from a pond. After recording the video, we stood 40m away and measured the maximum decibels produced by the frogs (Appendix 4: Playback Decibels). We separated the single video into three unique one-minute recordings and converted each to mp3 files.

Before conducting trials, all three exemplars of the LGD, VD, hornbill, and frog playbacks were downloaded onto mobile phones and tested with two first-generation Turtlebox® speakers. For each test, we positioned ourselves 40m away from the speaker. We adjusted the volume level until it matched the decibel levels observed during the recording of that exemplar or the observed decibel levels of wild hornbills and frogs (Appendix 4: Playback Decibels). The corresponding volume level for each exemplar was then noted and employed during trials.

To mitigate selection bias, we predetermined the playback order and exemplar for each commonly encountered cheetah before their first trial. For rare individuals, we assigned the order and exemplar for all six potential trials in the field before conducting their initial trial. Recognizing the challenge of conducting six trials with each cheetah, we ensured that each subject was exposed to a control playback (hornbill or frog) during one of their first two trials, with the hornbill serving as the control for VDs, cattle, and shoats, and the frog as the control for LGDs due to their novelty. The hornbill playback had a 75% chance of being assigned to the first or second trial, and the frog had a 25% chance, reflecting the relative frequency of treatment playbacks each control was paired with. Treatment playbacks were then randomly assigned accordingly. For example, if the hornbill was assigned to a subject's first trial, the second, third, and fourth trials randomly featured cattle, shoats, and VDs, with the frog and LGD randomly assigned to the fifth and sixth trials. No subject was exposed to the same playback more than once.

We defined a suitable subject as any solitary cheetah, a randomly selected coalition member, or the mother when cubs were present. The same coalition member was observed for all subsequent trials (up to six). When sub-adults separated from their mothers, we randomly selected one of the newly independent cheetahs from the group of siblings to be a new subject. Any playbacks they were exposed to while accompanying their mother were excluded from the possible playbacks they could still be exposed to. During one of the initial trials involving a mother cheetah and a very young cub, the mother fled so quickly following the playback that her cub could not keep up. Consequently, we established safety protocols wherein mother cheetahs could not be subjects until independent scientists at the Mara Predator Conservation Programme (MPCP) confirmed her cubs were at least three months old, ensuring they could flee with her if necessary. Additionally, if a cheetah was visibly injured (e.g., limping or with an open wound), we postponed trials with that subject until the injury healed, as injured cheetahs might exhibit altered responses (e.g., increased caution), and our playback could potentially have elevated the risk of further injury if the subject were to flee. We resumed trials with injured subjects after an independent evaluation from MPCP confirmed that they no longer displayed apparent behavioral alterations due to injury.

We opportunistically located individuals by searching known home ranges and receiving location reports from conservancy managers, rangers, and tourist guides. We aimed to balance our search for males and females, but females with cubs were more frequently located due to their relatively restricted movement and frequent tracking by tourist guides. At each encounter, individuals were identified by comparing their unique pelage to a database of known individuals maintained by MPCP [62, 63].

After locating a suitable subject, we observed them until specific behavioral and situational criteria were met. These criteria included the subject appearing relaxed, being more than two hours before sunset to allow sufficient time for trial execution, and no disturbances being visible to the observer. We defined ‘relaxed’ as the subject being inactive (e.g., lying down) and spending most of its time with closed eyes. Disturbances were defined as whenever the subject or coalition member was hunting or within 100m of a kill or when large herbivores (i.e., elephants, giraffes, buffalo, or hippo), other vehicles, or other large carnivores (i.e., lions, leopards, hyenas) were visible to the observer. In rare cases, trials were conducted when cattle or shoats were visible from over a kilometer away, provided they were moving away from the subject.

After ensuring the trial criteria were met, we positioned a Bluetooth speaker approximately 40m from the subject (35 – 49m). If any coalition members or cubs were present, we avoided moving between them and the subject. Cheetahs in the Maasai Mara are accustomed to tourist vehicles but not people on foot. Therefore, we positioned the speaker by quietly opening the vehicle door opposite the subject, placing it on the ground, and pointing it toward the subject without stepping out of the vehicle. We concealed the speaker behind low rocks or vegetation whenever possible, ensuring it would not obstruct the sound. Following the same guidelines as tourist vehicles observing cheetahs, we maneuvered the observation vehicle to a position in view of the subject, aiming for a 45-degree angle between the plane created by the subject and the speaker while ensuring the angle was less than 90 degrees (Figure 2-1). During this process, we observed no apparent behavioral reactions from any subjects.

To initiate a trial, we switched off the vehicle’s engine and started recording the subject with a video camera. B.S. used a Samsung Galaxy S21 Ultra, while C.H.S. used a Sony HDR-PJ780VE Handycam. We quietly spoke the date, the subject’s name, the playback and exemplar we used during that trial, and the direction (left/right) and distance the speaker was placed from the subject. Finally, we spoke the exact time we started a five-minute initial observation period (IOP). The trial was terminated if any disturbance (defined above) occurred or the subject moved (excluding sitting or standing without movement) during the IOP. If either happened, the reason for IOP termination was verbally noted, and we stopped video recording. Once the behavioral and situational criteria for a trial were again met, we started recording a new trial video and IOP.

At the end of each IOP, we played the assigned playback for that subject and trial. We continued to video-record the subject throughout the post-playback period (PPP) until the trial ended for one of the following reasons: a) The subject disappeared from the observer's view because they moved and settled in thick brush or fled the trial location. b) Other vehicles or domestic animals approached within 200m of the subject (this distance was determined based on our ability to detect vehicles and domestic animals from 100m away, reducing the chances of subjects reacting to actual disturbances before we ended the trial). c) The maximum PPP duration of one hour was met, resulting in a total observation time of 1 hour and 5 minutes (5 min IOP + 1 hour PPP). Upon a trial’s conclusion, the reason for ending the trial was quietly spoken before we stopped video recording.

We implemented a one-week washout period between trials for individuals to minimize potential carryover effects. We hoped this time would allow the subjects to encounter dogs, livestock, or other-human-associated stimuli before being exposed to another playback, reducing the chances of habituation.

Coding Videos: Three individuals coded each trial video for the subject’s behavior using BORIS®. Before coding the actual trial videos, we reviewed and discussed how to record each behavior (defined below) using a five-minute training video featuring a cheetah from the Maasai Mara. After this discussion, each person independently coded an additional five-minute training video to ensure a consistent understanding of the behavioral definitions. Each training video showed a cheetah displaying behaviors similar to those observed during the actual trials.

To evaluate intercoder reliability, we independently coded three trial videos assigned to each coder, resulting in nine trial videos being coded by two individuals. We compared how each coder measured activity and vigilance toward the speaker (defined below). We assessed measurement precision by calculating the average absolute difference between corresponding behavioral measures recorded by both individuals across all nine videos. We found an average measurement precision of 0.1% for activity and 1.5% for vigilance toward the speaker (Appendix 3: Intercoder Reliability – Table 2-A3-1).

To reduce measurement bias, we coded all trial videos blindly to the playback condition (i.e., LGD, VD, frog, hornbill) and without sound. Additionally, individuals who conducted specific trials did not code those trial videos. We aimed to code each trial video in a single session, including both the IOP (5min) and PPP (≤1 hour).

Measuring Behaviors: We measured five behavioral responses during each trial video: latency to initiate movement (latency), time spent moving toward the speaker, time spent moving away from the speaker, time spent active, and time spent vigilant toward the speaker. We defined latency as the time (min:sec) between playback initiation and the subject's first movement.

We measured time spent moving toward and away from the speaker only after playback initiation, throughout the entire PPP (≤1 hour), as our behavioral criteria for conducting a trial restricted movement during the IOP. We defined movement toward the speaker as any movement within an arc of less than 90° relative to the plane formed by the camera, subject, and the left or right edge of the video frame, depending on the direction of the speaker's placement (gray arc, Figure 2-1). Movement away from the speaker included movement in all other directions (white area, Figure 2-1). We did not measure speed or distance traveled.

We recorded time spent active and vigilant toward the speaker across the entire trial video (IOP + PPP). At the start of each trial, we required subjects to be relaxed (defined above). We defined a subject as active if it changed body posture or moved, such as sitting, standing, or walking, as these shifts often indicate changes in behavioral intention [47, 64-70]. We did not measure the direction of activity. In rare cases where obstacles obscured our view of the subject's body, we recorded activity as 'unknown' until visibility was restored.

Vigilance toward the speaker was measured by adapting the approach by Durant (2000), who measured cheetah vigilance toward lion and hyena playbacks [71]. We recorded a subject as vigilant if it directed its gaze beyond its body, associates, or immediate surroundings within the same <90° arc we used for movement toward the speaker (gray arc, Figure 2-1). This consistent measurement angle accounted for variability in speaker placement relative to the camera and allowed us to reliably observe the subject's eyes, aiding in our ability to confirm instances of vigilance when their gaze was directed toward the speaker. This approach minimized uncertainties in identifying vigilance, particularly when subjects directed their gaze away from the camera, making observing their eyes impossible. We did not record vigilance if the subject's eyes were closed or directed outside the defined arc (white area, Figure 2-1). In rare cases when obstacles obscured the observer's view of the subject's eyes while directing their gaze toward the speaker, we recorded vigilance as 'unknown' until visibility was restored.

Response Variables: From our five behavioral measures, we calculated three response variables for each subject and trial: movement response score, change in percent time active, and change in percent time vigilant toward the speaker.

We calculated the movement response score by subtracting the time the subject spent moving away from the speaker from the time spent moving toward it (net percent time moving toward or away from the speaker), then dividing this value by their latency to move. A greater negative score indicates faster, prolonged movement away from the speaker, suggesting *Deterrence*, while a greater positive score indicates faster, prolonged movement toward the speaker, suggesting *Attraction*. Individuals that did not move received a movement response score of zero.

We acknowledge that dividing net percent time moving by other factors, such as PPP duration instead of latency, would also provide insights into individual responses. However, we selected latency due to its conservative nature and its use in prior studies [71] . Using PPP duration might skew response intensity if trials ended early due to external factors (e.g., approaching vehicles), potentially exaggerating movement effects. Conversely, latency may underestimate response intensity if subjects remained stationary and their trials ended early, eliminating the possibility of us observing movement due to our playback. This conservative measure makes it less likely to find a false effect.

We calculated changes in percent time active and vigilant toward the speaker across two timescales: the entire PPP and consecutive five-minute post-playback intervals (PPIs; PPI 1 = 0 – 5 min post-playback, PPI 2 = 5 – 10 min, etc.). The five-minute interval mirrors the IOP's duration, providing a direct comparison and allowing us to analyze how individuals exhibited each behavior over time. We calculated changes by subtracting each behavior's duration during the IOP from the PPP or each PPI. For individual PPIs, we required a minimum observation of 30 seconds. For example, if a PPP lasted 10:20 min:sec, we analyzed changes for the entire PPP, PPI 1, and PPI 2 but omitted PPI 3 due to its shorter duration.

Analysis

Statical Significance: We applied Bonferroni correction to account for multiple comparisons, with a p-value of 0.05 – 0.01 considered suggestive and $p < 0.01$ considered significant [61, 72, 73].

Movement: We used within-cheetah and between-cheetah analyses to test for *Deterrence* or *Attraction*. We began with one-sample Wilcoxon signed rank tests for within-cheetah tests to determine if median movement response scores differed significantly from zero after LGD, VD, frog, or hornbill playbacks (Table 2-1). We then applied a modified Hills-Armitage approach to compare movement scores across playback conditions (LGD vs. frog, VD vs. hornbill, LGD vs. VD) [74]. In this approach, we grouped individuals exposed to each playback pair based on the sequence in which they were exposed to each (e.g., LGD first and frog second, frog first and LGD second), calculated the individual's difference in movement response scores between the playbacks, and used two-sample Wilcoxon rank sum tests to compare the median difference between groups (Table 2-1). Due to logistical constraints, some within-cheetah tests had reduced sample sizes as not all cheetahs were exposed to each playback pair. For between-cheetah tests, we used Wilcoxon rank sum tests to compare median movement response scores between all cheetahs exposed to each playback in each comparison (Table 2-1).

Vigilance & Activity: We used within-cheetah and between-cheetah analyses to examine changes in activity and vigilance toward the speaker following LGD, VD, frog, and hornbill playbacks. For within-cheetah tests, we began with two-sample Wilcoxon signed-rank tests to determine if the median percent time active and vigilant during PPI 1 and the entire PPP differed from the median percent time during the IOP of the same trial. To compare changes in activity and vigilance between playbacks, we calculated the change in each behavior across both timescales (PPI 1 and PPP) by subtracting the percent time each behavior was exhibited during the IOP from the percent time exhibited during PPI 1 and PPP. We then applied the modified Hills-Armitage approach (described above) and Wilcoxon rank sum tests to compare the median changes across playback conditions (LGD vs. frog, VD vs. hornbill, LGD vs. VD) [74]. Due to logistical constraints, some within-cheetah tests had reduced sample sizes when individuals were not exposed to each playback pair. For between-cheetah tests, we used Wilcoxon rank sum tests to compare median changes in activity and vigilance between all cheetahs exposed to each playback in each comparison. If statistically significant changes in either behavior were found during PPI 1, we applied the same analysis methods to subsequent PPIs until no further differences were detected.

Habituation: We evaluated habituation by testing whether individuals exposed to three or more playbacks (n = 9; six total playbacks, including cattle, shoat, and hornbill) exhibited decreasing changes in vigilance toward the speaker and activity during PPI 1 and the entire PPP of each trial as they were exposed to more playbacks. Individuals exposed to three or fewer playbacks (n = 3) were excluded due to the increasing likelihood of habituation with greater exposure. To encompass the potential habituation of our methods (e.g., speaker placement), we considered the total number of playbacks (including treatment and control playbacks) rather than just the treatment playbacks. We used Spearman’s rank correlation rho tests to initially examine whether individual changes in either behavior during PPI 1 or the entire PPP decreased with increased exposure to more playbacks (Appendix 1: Habituation – Table 2-A1-1). Subsequently, we used one-sample Wilcoxon signed rank tests to examine whether the slope parameters for each behavior change during the two timescales statistically differed from zero, with negative slope parameters indicating reduced changes in behavior as individuals were exposed to more playbacks (Appendix 1: Habituation – Table 2-A1-2).

Order Effect: We assessed whether the sequence of playback exposure influenced cheetah responses using a modified Hills-Armitage approach [74]. For within-cheetah tests of each treatment stimulus (LGD, VD), we categorized individuals into Treatment-First and Control-First groups based on the initial stimulus they encountered (treatment or control: frog or hornbill). While some cheetahs were exposed to other stimuli in between, our randomized stimuli sequence and habituation assessment increased our confidence that intermediate exposures had minimal influence on responses. For each individual, we calculated the difference in change for vigilance toward the speaker and activity during PPI 1 and the entire PPP following exposure to treatment and control stimuli (treatment – control). We then used a two-sample Wilcoxon rank sum test to compare median differences in behavior change between Treatment-First and Control-First groups Appendix 1: Order-Effect – Table 2-A2-1). Any statistical difference in behavior change during any period suggests potential within-subject order effects for that treatment stimulus.

Results

We observed 15 individuals across 40 audio playback trials. Eleven trials used a livestock guarding dog (LGD) playback, nine used a village dog (VD) playback, eight used a frog playback, and 12 used a hornbill playback. Median post-playback period (PPP) duration varied by condition, with the shortest following LGDs (41:02 min; Interquartile Range [IQR]: 24:20–59:56), followed by VDs (59:35; IQR: 25:46–60:00), hornbills (50:43; IQR: 15:51–60:00), and frogs (54:26; IQR: 20:16–60:00). However, these differences were not statistically significant for either comparison of treatment and control conditions, LGD and Frog (Wilcoxon rank sum test: $W = 37$, $p = 0.58$) or VD and hornbill ($W = 56$, $p = 0.91$). Therefore, we infer that our playbacks did not elicit flight in most cheetahs, which would have significantly shortened the PPP duration.

Livestock Guarding Dogs (LGDs):

Movement: Across cheetah subjects, median movement response scores did not differ from zero (no movement) following the LGD or frog playbacks (Table 2-1). However, the median movement response scores following LGD playbacks approached suggestive levels of significance. Additionally, within- and between-cheetah comparisons of median movement response scores between LGD and frog conditions showed no significant differences (Table 2-1).

Table 2-1: Comparisons of median movement response scores following livestock guarding dog (LGD), village dog (VD), frog, and hornbill playbacks. Within-cheetah tests examine if individual movement response scores differed from zero after each playback. Within-cheetah comparisons of conditions examine the differences in movement response scores for individual cheetahs that received both conditions. Between-cheetah comparisons of conditions examine the differences in movement response scores for all cheetahs exposed to both conditions.

Stimulus, Response Variable	Movement Response Score		
Within-Subject Test (n of individuals)	**Median (Q1 to Q3)**	**V =**	**p =**
LGD (n = 11)	0 (- 0.13 to 0)	0	0.06
Village Dogs (n = 9)	0 (0 to 0)	2	0.1
Frog (n = 8)	0 (- 0.01 to 0)	3	0.58
Hornbill (n = 12)	0 (- 0.01 to 0)	0	0.1
Within-Cheetah Comparisons of Conditions (n of individuals)	**Median (Q1 to Q3) Difference**	**W =**	**p =**
LGD vs. Frog (n = 8)	0 (- 0.14 to 0)	W = 3	0.36
VD vs. Hornbill (n = 8)	0 (0 to +0.08)	W = 7	0.58
LGD vs. VD (n = 8)	0 (-0.08 to 0)	W = 2	0.36
Between-Cheetah Comparisons of Conditions	**Median Difference**	**W =**	**p =**
LGD vs. Frog	0	59	0.2
VD vs. Hornbill	0	38	0.16
LGD vs. VD	0	70	0.07

We included the median and interquartile range (IQR: 1st to 3rd quartile) of individual movement response scores for within-cheetah tests and comparisons.
We analyzed within-cheetah movement response scores using Wilcoxon signed-rank tests.
We analyzed within-cheetah comparisons using the Hills-Armitage approach [74] and Wilcoxon rank sum tests, excluding individuals who received only one playback.
We analyzed between-cheetah comparisons using Wilcoxon rank sum tests.

Five of 11 individuals moved following the LGD playback, all exhibiting net movement away from the speaker. Four fled the trial location, ending their PPP early, while one remained in view throughout (Figure 2-2). In contrast, four of eight individuals moved after the frog playback, with two exhibiting net movement away from the speaker and two exhibiting net movement toward it (Figure 2-2). Only one individual fled the trial location, while the others remained in view for their entire PPP. Additionally, individuals spent more time moving away from the speaker after the LGD playback (mean ± SE: -4% ± 3) and had a shorter latency to move (42:12 ± 7:35) than after frog playbacks (net movement: -1% ± 1; latency: 42 ± 7:52; Figure 2-2). Although statistical tests comparing individual net movement (V = 4, p = 0.42) and latency (V = 5, 0.59) following LGD and frog playbacks were insignificant, the proportion of individuals who moved after each, and the effect sizes of both variables suggest that the LGD playback influenced some cheetahs. Given the consistent movement away from the speaker, these results provide some evidence for *Deterrence* by LGDs.

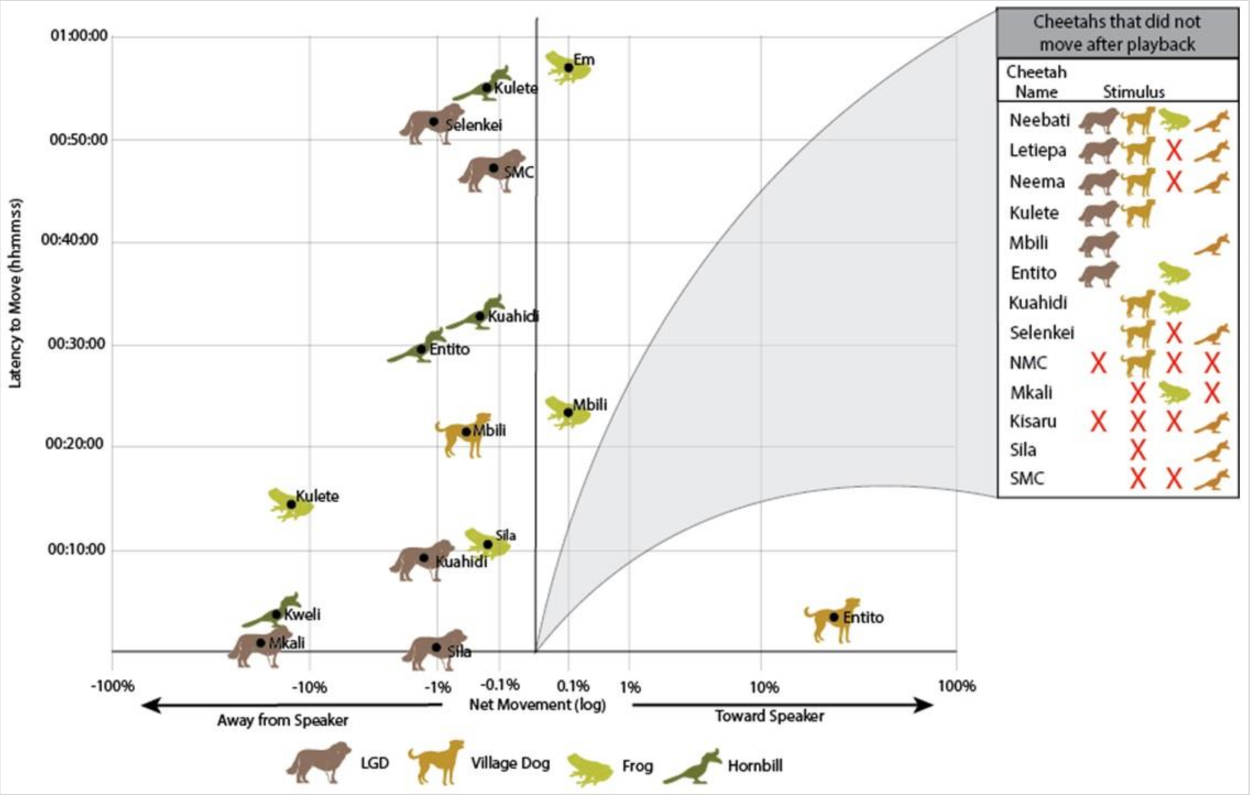

Figure 2-2: Cheetah movements following audio playbacks of livestock guarding dogs (LGD: dark brown), village dogs (VD: brown), frogs (green), or hornbills (dark green). Individual cheetahs (circles with names), net percent time moving away from or toward the speaker (x-axis), and latency to move (y-axis) after each playback. Individuals on the left of the graph exhibited net movement away from the speaker, while individuals on the right exhibited net movement toward the speaker. Individuals who did not move after each playback are listed in the box in the top right. Red Xs in the box indicate the individual was not exposed to that playback.

Activity & Vigilance: Cheetahs exposed to the LGDs were statistically more active and vigilant during PPI 1 and PPI 2 than during the IOP (Table 2-2, Figure 2-3). Although some cheetahs maintained elevated activity or vigilance into PPI 3, within-cheetah tests suggest most returned to similar rates of each behavior as the IOP during this interval (Table 2-3). Therefore, neither behavior was analyzed during subsequent PPIs. When considering the entire PPP, individuals were significantly more active after

LGDs, and while some were more vigilant, within-cheetah tests revealed this change was not statistically different (Table 2-2, Figure 2-4). In contrast, frogs did not elicit statistical changes in either behavior during any period (Table 2-2).

Table 2-2: Comparisons of the changes in activity and vigilance toward the speaker following livestock guarding dog (LGD), village dog (VD), frog, and hornbill playbacks. Within-cheetah tests examine if individuals exhibited a greater rate of either behavior during post-playback intervals (PPI 1, PPI 2, PPI 3) or the entire post-playback period (PPP) after each playback than during the initial observation period (IOP). Within-cheetah comparisons of conditions examine the differences in each behavior for individual cheetahs that received both conditions. Between-subject comparisons of conditions examine the differences in each behavior for all cheetahs exposed to both conditions.

Stimulus, PPIs, PPP / Behavior		**Activity**			**Vigilant Toward the Speaker**		
Within-Subject Tests After vs. IOP (n of individuals)		**Median %** (Q1 to Q3)	**V =**	**p =**	**Median %** (Q1 to Q3)	**V =**	**p =**
LGD	**PPI 1** (n = 11)	+62 (+30 to +90)	0	0.01**	+46 (+28 to +58)	0	0.001**
	PPI 2 (n = 11)	+2 (0 to 32)	0	0.04*	+16 (+5 to +29)	6	0.01**
	PPI 3 (n = 9)	0 (0to 0)	0	1	+2 (-6 to +8)	15.5	0.78
	PPP (n = 11)	+13 (+4 to +31)	0	0.01**	+9 (0 to +22)	9	0.07
VD	**PPI 1** (n = 9)	+43 (0 to +55)	0	0.04*	+32 (+17 to +47)	0	0.004**
	PPI 2 (n = 8)	0 (0 to 0)	0	1	+13 (0 to +27)	5.5	0.09
	PPP (n = 9)	+10 (+2 to +18)	0	0.01**	+6 (-2 to +10)	11	0.19
Frog	**PPI 1** (n = 8)	0 (-5 to 0)	5	0.42	+1 (0 to +6)	5	0.29
	PPP (n = 8)	0 (-5 to +1)	8	1	0 (-7 to +9)	24.5	0.46
Hornbill	**PPI 1** (n = 12)	0 (0 to 0)	1	0.4	+3 (-2 to +18)	19	0.13
	PPP (n = 12)	+1 (0 to +3)	5	0.08	+2 (-1 to +10)	19.5	0.14
Within-Cheetah Comparisons of Conditions (n of individuals)		**Difference in Median %** (Q1 to Q3)	**W =**	**p =**	**Difference in Median %** (Q1 to Q3)	**W =**	**p =**
LGD vs. Frog	**PPI 1** (n = 7)	+81 (+38 to +91)	11.5	0.07	+45 (+19 to +60)	12	0.06
	PPI 2 (n = 7)	+39 (0 to +67)	11	0.1	+8 (+5 to +38)	10	0.23
	PPP (n = 7)	+33 (0 to +75)	10.5	0.15	+9 (-7 to +46)	9	0.4
VD vs. Hornbill	**PPI 1** (n = 8)	+13 (0 to +59)	2	0.09	+12 (+4 to +29)	0	0.02*
	PPI 2 (n = 8)	0 (0 to 0)	3	1	+1 (-6 to +20)	13	0.55
	PPP (n = 8)	+5 (+1 to +13)	6	0.2	-1 (-10 to +12)	18	1
	PPI 1 (n = 8)	+5 (-13 to +38)	10	0.55	+5 (-19 to +22)	15	0.74

LGD vs. VD	**PPP** (n = 8)	-5 (-11 to +8)	18.5	0.5	+3 (-14 to +15)	17	0.94
Between-Cheetah Comparisons of Conditions		**Difference in Median %**	**W =**	**p =**	**Difference in Median %**	**W =**	**p =**
LGD vs. Frog	**PPI 1**	+62	10.5	0.005**	+45	4.5	0.001**
	PPI 2	+2	18.5	0.03*	+16	16	0.04*
	PPI 3	0	28	0.7	+6	26	0.6
	PPP	+13	18.5	0.04*	+9	26	0.15
VD vs. Hornbill	**PPI 1**	+43	25.5	0.03*	+29	17.5	0.01**
	PPI 2	0	54	1	+14	37.5	0.26
	PPP	+9	28	0.07	+4	54	1
LGD vs. VD	**PPI 1**	+19	44.5	0.73	+14	40	0.5
	PPP	+3	28.5	0.11	+3	35	0.3

Sample sizes varied between PPI 1 and PPI 2 for cattle and shoat playbacks due to the PPP ending during PPI 1 in some trials (see methods).
We did not test median behavior changes in PPI 3 for cattle and shoat playbacks or in PPI 2 for the hornbill playback, as prior PPIs showed no statistical changes in either behavior.
We analyzed within-cheetah tests using Wilcoxon signed-rank tests.
We analyzed within-cheetah comparisons of conditions using the Hills-Armitage approach [74] and Wilcoxon rank sum tests, excluding individuals who received only one playback.
We analyzed between-cheetah comparisons of conditions using Wilcoxon rank sum tests.
** Bonferroni corrections signifying a significant behavior change, p-value ≤ 0.01.
* Bonferroni corrections signifying a suggestive behavior change, p-value ≤ 0.05 & > 0.01.

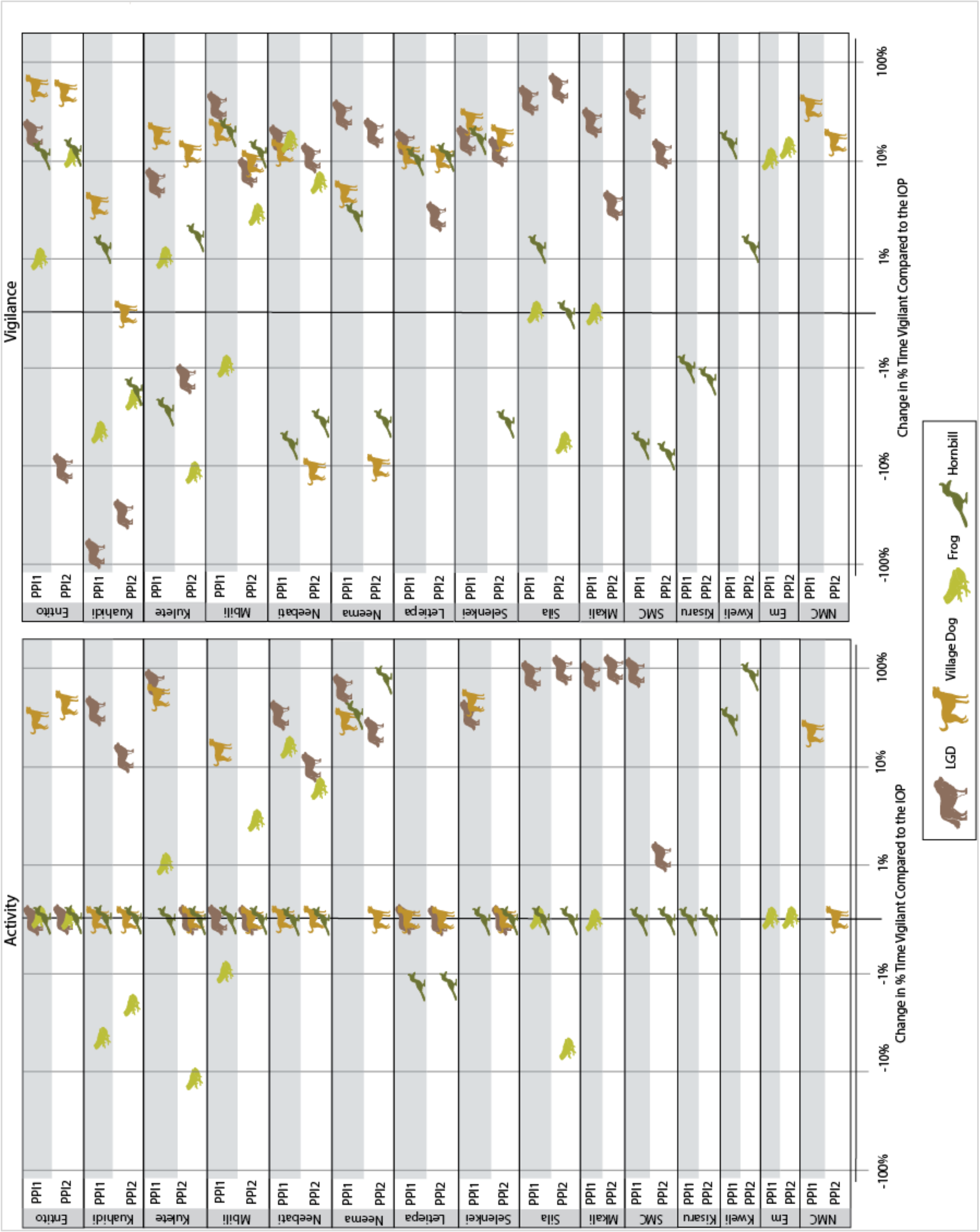

Figure 2-3: Individual changes in activity (left frame) and vigilance toward the speaker (right frame) between post-playback interval 1 (PPI 1) and 2 (PPI 2) and the initial observation period (IOP) after the livestock guarding dog (LGD; dark brown), village dog (VD; brown), frog (green), or hornbill (dark green) playbacks. A positive change indicates that the individual exhibited that behavior more during that PPI than during the IOP. A negative change indicates that the individual exhibited that behavior more during the IOP than the PPI.

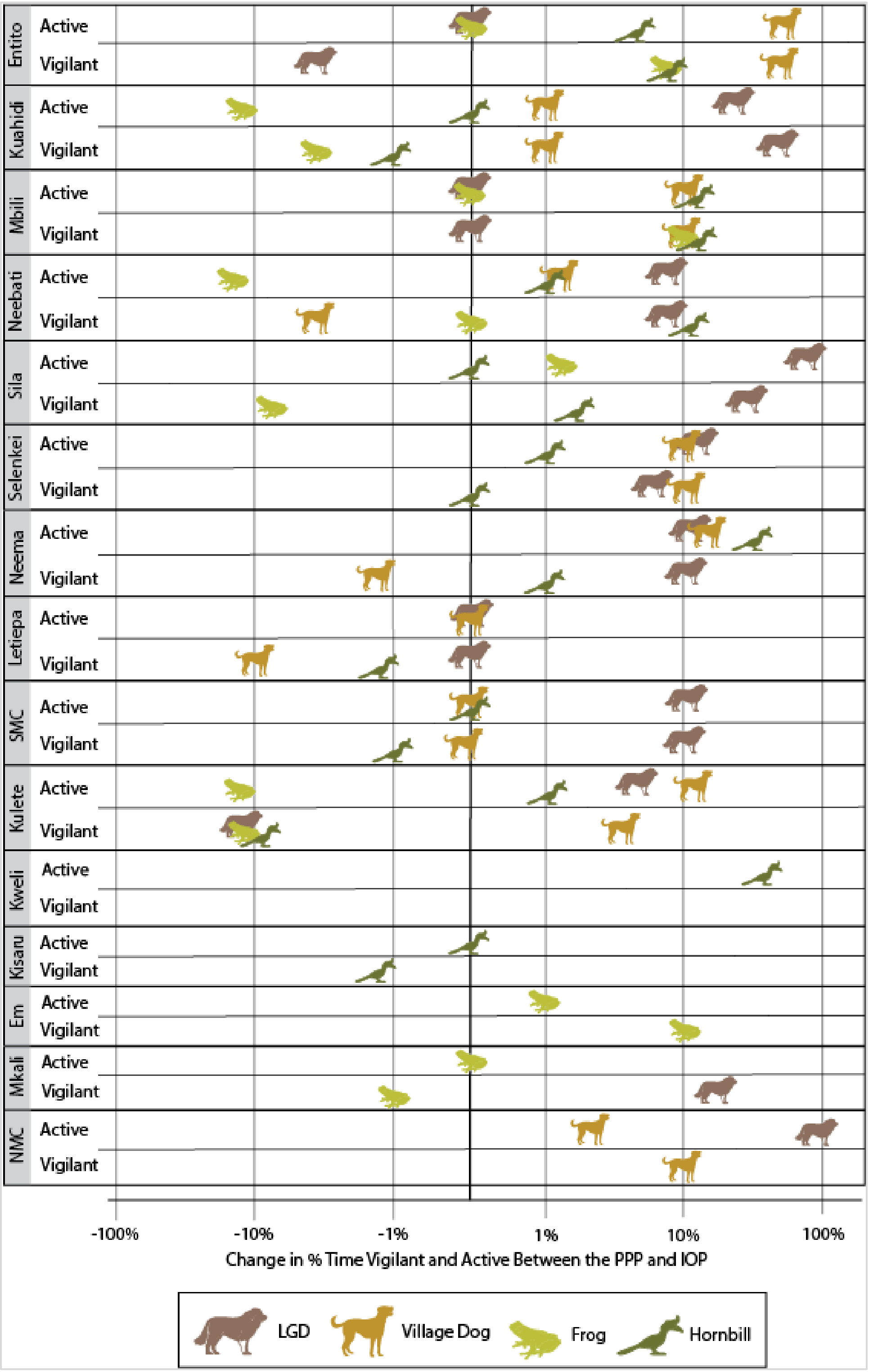

Figure 2-4: Individual changes in vigilance toward the speaker and activity between the post-playback period (PPP) and Initial Observation Period (IOP) after the livestock guarding dog (LGD; dark brown), village dog (VD; brown), frog (light green), or hornbill playbacks (dark green). A positive change indicates that the individual exhibited that behavior more during the PPP than during the IOP. A negative change indicates that the individual exhibited that behavior more during the IOP than the PPP.

Within-cheetah comparisons revealed that individuals exposed to LGDs and frogs exhibited a greater increase in activity and vigilance during PPI 1 and throughout the entire PPP following LGDs (Figure 2-2). However, these differences did not meet statistical thresholds (Table 2-2). By PPI 2, individual changes in activity and vigilance following both playbacks were similar (Table 2-2). In contrast, between-cheetah comparisons showed that cheetahs exposed to LGDs exhibited significantly greater increases in activity and vigilance during PPI 1, with both behaviors remaining suggestively higher during PPI 2 (Table 2-2, Figure 2-3). By PPI 3, differences in both behaviors no longer met statistical thresholds (Table 2-2, Figure 2-3), suggesting they returned to baseline levels of both behaviors during this interval. When considering the entire PPP, cheetahs exposed to LGDs exhibited suggestively greater increases in activity but not vigilance (Table 2-2, Figure 2-4). Therefore, while both comparison methods suggest greater salience and arousal from LGDs, between-cheetah comparisons indicate more robust and sustained arousal compared to the control.

Village Dogs (VDs):

Movement: Across cheetah subjects, median movement response scores did not differ from zero (indicating no movement) following VD and hornbill playbacks (Table 2-1). Additionally, within- and between-cheetah comparisons of median movement response scores between VD and hornbill and VD and LGD conditions showed no significant differences (Table 2-1).

Only two of nine individuals moved following the VD playback, with one exhibiting net movement away from the speaker and one exhibiting net movement toward it (Figure 2-1). In comparison, four of 12 individuals moved following the hornbill playback, and five of 11 moved after the LGD playback, all exhibiting net movement away from the speaker. Individuals spent more time moving toward the speaker after the VD playback (+4% ± 3) and had a longer mean latency to move (48:40 min:sec ± 7:00) than after the LGD (net movement: -4% ± 5; latency: 42:12 ± 7:35) or hornbill playbacks (net movement: -2% ± 2; latency: 49:28 min:sec ± 5:10; Figure 2-2). Statistical tests comparing individual net movement (V = 7, p = 0.58) and latency to move (V = 4, p = 0.86) following VD and hornbill playbacks were insignificant, and the effect sizes provided no clear indication of the VD playback influencing a greater response. Thus, these results provide little evidence for *Deterrence* or *Attraction* by VDs.

Activity & Vigilance: Individuals were more active and vigilant toward the speaker during PPI 1 following the VD playback than during the IOP, with within-cheetah tests showing a suggestive increase in activity and a significant increase in vigilance (Table 2-2, Figure 2-3). By PPI 2, changes in both behaviors returned to levels similar to the IOP (Table 2-2). Therefore, neither behavior was analyzed during subsequent PPIs. When considering the entire PPP, individuals exhibited higher levels of activity and vigilance than during the IOP (Figure 2-4). However, within-subject tests indicated this difference was only significant for activity (Table 2-2). In contrast, individuals exposed to the hornbill playback exhibited minimal or no changes in activity or vigilance across all periods (Table 2-2).

Within-cheetah comparisons showed that individuals exhibited a greater increase in activity and vigilance during PPI 1 after VDs than after hornbills, with activity changes not reaching statistical significance and vigilance changes meeting the suggestive threshold (Table 2-2, Figure 2-2). By PPI 2, changes in both behaviors were similar for both playbacks (Table 2-2). Both behavior changes were similar across both playbacks when considering the entire PPP (Table 2-2). Between-cheetah comparisons indicated that those exposed to VDs showed greater increases in activity and vigilance during PPI 1 than those exposed to hornbills, with a suggestive increase in activity and a significant increase in vigilance (Table 2-2). During PPI 2, vigilance remained higher in those exposed to VDs, though not statistically significant, while activity changes were similar across both playbacks (Table 2-2). Over the entire PPP, individuals exposed to VDs showed a slightly greater activity increase than those exposed to hornbills. However, this was not statistically significant, and vigilance was similar across both groups (Table 2-2). Therefore, both comparison methods suggest VDs were more salient and likely to arouse cheetahs in the first five minutes following playback than the control.

Both within-cheetah and between-cheetah comparisons indicated that cheetahs were more active and vigilant during PPI 1 after LGDs than after VDs, though these differences were not statistically significant. Across the entire PPP, changes in both behaviors were similar between the two playbacks (Table 2-2). This suggests that LGDs may have been slightly more salient, causing greater initial arousal than the VD playback, but any difference in behavioral effects was minimal and short-lived.

Habituation and Order Effects:

Individuals exposed to multiple playbacks exhibited similar changes in activity and vigilance, regardless of the number of playbacks they were exposed to (Appendix 1: Habituation – Table 2-A1-1 & 2-A1-2). Individual comparisons revealed that cheetahs exhibited similar changes in activity and vigilance following the LGD and frog playbacks, or MBD and frogs, irrespective of the order in which they were exposed to each (Appendix 2: Order-Effects – Table 2-A2-1). Therefore, we found no evidence of habituation or order effects.

Discussion

We tested contrasting hypotheses – *Deterrence* and *Attraction* – to assess whether wild cheetahs are deterred or attracted to two breeds of domestic dogs: livestock guarding dogs (LGDs) and village dogs (VDs). To test these hypotheses, we directly observed individual cheetahs' short-term responses to experimentally manipulated audio playbacks simulating the presence of LGDs, VDs, and two control animals (frogs and hornbills). Our findings indicate that both dog playbacks were salient, eliciting increased activity (e.g., changes in body posture and movement) and vigilance. These changes were particularly pronounced within the first five minutes after each playback and persisted for five more minutes after LGDs. Despite their salience, only five of eleven cheetahs moved away from the speaker after the LGD playback, while the majority remained stationary after the VD, frog, and hornbill playbacks. Therefore, our results provide only some evidence supporting *Deterrence* for LGDs and no evidence supporting *Deterrence* or *Attraction* for VDs.

Movement is our most informative measure of behavioral response, offering the most apparent distinction between *Deterrence* and *Attraction*. Movement requires greater energy expenditure compared to other behaviors, and can increase exposure to potential risks associated with the stimulus or other nearby threats. In previous studies on carnivores, including cheetahs, movement away from a speaker has been interpreted as deterrence in response to playbacks of known threats [47, 68, 69, 71, 75]. Conversely, movement toward the speaker after playbacks of prey has been used to infer attraction in other carnivores [57, 58, 76, 77]. To our knowledge, no study has simultaneously measured movement toward and away from stimuli of unknown threat or prey value. However, our approach provides a framework to differentiate between these responses.

For individuals who did not move, we rely on changes in activity and vigilance to infer salience and lower-cost responses to the playbacks. Vigilance reflects low-cost information gathering, making cheetahs only slightly more conspicuous to potential observers [55, 60, 78-81]. By contrast, heightened activity suggests a greater arousal than vigilance alone. For example, sitting up following a playback would change a cheetah's conspicuousness but also allow longer-distance detection and prepare the individual for flight or approach if appropriate. Furthermore, some behavioral patterns might explain individual perceptions of the playbacks. Cheetahs who are more vigilant and active are reported to be more likely to initiate hunts [55]. In contrast, individuals who remain prone but increase vigilance have been described as acting uneasy and potentially trying to detect approaching threats [55]. Therefore, while activity and vigilance without movement cannot definitively differentiate *Deterrence* from *Attraction,* they still allow us to assess the salience of stimuli by comparing responses to treatment playbacks (LGD and VD) against non-threatening controls (frog and hornbill).

Livestock Guarding Dogs (LGDs): Five of the eleven cheetahs – Kuahidi, Mkali, Selenkei, Sila, and Sila's male cub (SMC) – moved away from the speaker following the LGD playback, with four disappearing from view within the one-hour post-playback period (PPP; Figure 2-2). In comparison, while four of eight cheetahs moved after the frog control, only two moved away from the speaker, and just one disappeared from view. These results provide the first direct evidence supporting the assumption that LGDs may help protect livestock by deterring individual cheetahs in the short term [28, 29, 37-40, 50, 82]. Furthermore, within-subject comparisons of individual responses to both LGD and frog playbacks offer robust support that LGDs can directly cause *Deterrence*, at least in some cheetahs.

Kuahidi and Mkali's responses provide the clearest evidence for deterrence. Both moved away from the speaker after LGDs, and neither moved after frogs (Figure 2-2). However, their retreats appeared cautious and deliberate rather than rapid or sudden attempts at escape. Mkali reacted quickly, moving before the LGD playback ended (latency = 00:56 min), but he took over seven minutes to cover approximately 150 meters before disappearing from view. As he retreated, he frequently scanned the direction he was heading (away from the speaker) and, on several occasions, stopped to turn back and scan the area within the speaker's vicinity. By contrast, Kuahidi did not move until almost ten minutes after the LGD playback (latency = 9:22), suggesting she perceived the threat as less immediate than Mkali or needed to gather more information before retreating. Once she did move, however, she disappeared from view in under thirty seconds, indicating a swift movement to avoid detection by the simulated LGDs, which she could not locate. Thus, it seems more likely that Kuahidi's delayed movement was due to her feeling more secure in her initial location, leading her to gather more information before exposing herself [83]. In contrast, Mkali may have felt more exposed, prompting an immediate retreat while still assessing his surroundings. Therefore, we infer that the sound playbacks of LGDs themselves are not sufficiently salient to trigger a rapid escape. Instead, the behavior of these individuals reflects a strategic response to gathering information about their surroundings before moving away.

Sila's response was particularly intriguing, but we ultimately interpret it as additional evidence of deterrence. Unlike the two individuals above, Sila moved away from the speaker after the frog played back. Still, her overall response suggests this movement was more likely a minor adjustment rather than a reaction to the frogs. She did not move until well after the playback ended (latency = 10:33 min) and quickly lay back down for the remainder of her observation period. Additionally, her vigilance toward the speaker decreased after the frog playback, indicating it was not sufficiently salient to elicit even a low-cost response (Figures 2-3 & 2-4). In contrast, she moved within 34s of the LGD playbacks' initiation (Figure 2-2). Initially, she moved toward the speaker, even passing it within a meter without showing any apparent awareness of it. She continued moving approximately 50 meters beyond the speaker (observer estimate), frequently pausing to scan in the original direction of the speaker, even though the speaker was now behind her (e.g., in the direction that had been the background of the speaker). During this time, she did not exhibit behaviors typically associated with hunting or concealment, such as stalking or crouching. Instead, her movements appeared investigative, as she repeatedly shifted to different vantage points to gain a better view. About 30 minutes later, she turned and retraced her steps to her original location (within one meter of where she was when the playback began), again passing close to the speaker without showing any apparent awareness of it. Upon returning, she briefly laid back down (<30 seconds), continued scanning toward the speaker, and then retreated directly away from the speaker. Over the next 10 minutes, she gradually moved farther away, intermittently stopping to scan in the direction of the speaker until she disappeared from view. This response was unique among all observations, representing an extreme example of a cheetah investigating the potential presence of LGDs or any human-associated stimuli. Unable to visually confirm the dog’s presence, Sila searched for the sound’s source. Her initial approach and vigilance could suggest she perceived the LGD presence as potentially beneficial, either as prey or interpreting it as a cue for nearby livestock (village dogs often accompany livestock outside the conservancies). However, in our opinion, her continued scanning and eventual retreat seemed to indicate her response was an attempt at locating a potential threat, akin to how humans visually track dangerous animals to mitigate future risks. Nevertheless, her response highlights how our method cannot always definitively interpret investigative behavior, underscoring the complexity involved in analyzing behavioral responses to playbacks.

Selenkei and SMC provide additional evidence supporting deterrence by LGDs. Neither individual was exposed to the frog playback, preventing direct comparisons between the novel stimuli. However, since no individual exhibited significant behavioral effects in response to frogs, this lack of exposure is unlikely to influence our inferences. Additionally, both individuals were exposed to and did not move following the hornbill playback, providing a control for comparison. Neither Selenkei nor SMC moved immediately after LGDs, but both were more active and vigilant in the first five minutes than after hornbills (Figure 2-3). They also maintained greater vigilance throughout their observation periods following the LGD playback (Figure 2-4). These behaviors suggest that while neither individual perceived an immediate need to flee, the LGD playback promoted continuous monitoring of their surroundings. Ultimately, both individuals moved away from the speaker during their observation periods, with SMC moving after 47:23 and disappearing from view shortly after and Selenkei retreating after 51:57 but remaining visible. This combination of delayed movement and heightened vigilance indicates the potential presence of LGDs influenced their behavior and movement direction. Thus, Selenkei and SMC appeared to perceive the possible presence of LGDs as less threatening than other cheetahs, but their overall responses still indicate deterrence.

Despite individual variation, all five cheetahs that moved after the LGD playback retreated cautiously, suggesting they perceive LGDs as threatening but not severe enough to justify reckless flight. Multiple factors may explain this behavior. First, the sound of LGDs barking was novel to the cheetahs, potentially deterring them due to its unfamiliarity. While using the frog playback, also a novel sound, strengthens confidence in our inferences, cheetahs may be naturally cautious around new noises associated with potentially dangerous animals. Although LGD barks are acoustically similar to VD barks, their louder and deeper quality may instinctively trigger fear, as novel yet generalizable threats can do in intelligent animals.

Second, cheetahs may perceive LGDs similarly to other large carnivores known to injure and kill cheetahs. A study using lion and hyena playbacks found a more significant proportion of cheetahs moved within the first 30 minutes compared to our LGD playbacks [71], indicating that cheetahs may assess LGDs as comparatively less threatening. However, even in response to lions and hyenas, some cheetahs did not flee immediately, aligning with our observations and indicating a tendency for cheetahs to gather more information before retreating from a threat. This cautious strategy may reflect learned or instinctive behaviors to mitigate risks. Hastily fleeing without assessing their surroundings could increase conspicuousness to the detected threat or additional predators approaching from other directions. If accurate, this response suggests that using movement away from the speaker as the sole indicator of

Deterrence may underestimate the number of cheetahs perceiving LGDs as threats. For example, individuals who remained stationary after the LGD playback may have refrained from moving to minimize exposure despite perceiving a threat. However, given our playbacks presented no actual threats, such individuals would likely have eventually concluded that there was minimal risk and retreated. Nevertheless, this possibility implies that we may have underestimated the number of cheetahs perceiving LGDs as significant threats. Our observations of increased activity and vigilance provide valuable additional insights into how individuals who did not move perceived LGD presence.

Seven individuals – Entito, Kulete, Leteipa, Mbili, Neebati, Neema, and Sila’s male cub (SMC) – did not move after the LGD playback. All exhibited increased vigilance toward the speaker in the first five minutes, suggesting the playback was salient. However, only three – Kulete, Neebati, and Neema – displayed heightened activity. Neebati and Neema remained more active and vigilant for ten minutes before returning to baseline levels, while Kulete was only more active and vigilant for five minutes. Increased activity and vigilance, particularly sitting up, correlate with a higher likelihood of hunting [55], suggesting that these individuals associated LGDs with potential benefits, such as perceiving LGDs as prey or as indicators of nearby livestock. However, the lack of movement toward the speaker and evidence that other individuals were deterred suggest these individuals may also have been assessing LGDs as potential threats. Furthermore, descriptions of cheetahs exhibiting increased vigilance while lying down, as seen in the other four individuals, suggest this behavior helps detect approaching threats, reinforcing the likelihood that they perceived LGDs as threatening. Individual perceptions of LGDs may differ, with some viewing them as beneficial and others as threats. Differences in responses may also reflect external factors. For example, individuals who increased activity may have been lying in taller grass, requiring them to sit or stand to assess the LGDs’ presence, while others could remain prone. Therefore, it remains challenging to confidently interpret varying responses without further observations. Regardless of their perceptions, all seven individuals returned to baseline levels of activity and vigilance within ten minutes. This suggests that whether assessing LGDs as a potential benefit or threat, their initial arousal was short-lived in the absence of further confirmation of LGD presence.

Individual variation in reactions to LGDs might reflect past experiences with dogs, individual temperament, attributes of the calls, cover, or salience of the stimuli. While the movement of some individuals away from the speaker after the LGD playback provides some support for *Deterrence,* the lack of movement by others suggests that the presence of LGDs may not deter all cheetahs. For those who did not move, it seems more likely they perceived the LGD presence as a potential threat but did not find it significant enough to prompt immediate movement. These individuals may be more accustomed to the presence of dogs and, therefore, require more salient stimuli (i.e., visual confirmation) to trigger a response severe enough to cause retreat. However, the behavior of a few individuals also suggests the possibility that they perceived the LGD playback as potentially beneficial, indicating that not all cheetahs may uniformly view LGDs as a threat during initial encounters. Curiosity has been noted in intelligent animals, and carnivores are no exception. Given these varied responses and the lack of clear evidence, we recommend that future research further investigate the potential variation in individual short-term reactions to the presence of LGDs, considering factors such as past experiences, temperament, and the nature of the stimuli.

Village Dogs (VDs): A smaller proportion of cheetahs moved following the VDs (n = 2 of 9) compared to hornbills (n = 4 of 12) or LGDs (n = 5 of 11). This suggests that playbacks of VDs were not salient enough to justify movement, supporting the null hypothesis. All five individuals who moved away from the speaker after LGDs were also exposed to VDs, yet none moved away. This highlights a distinct difference in response to each dog breed that is unlikely due to the novelty of LGDs (see above comparison with frogs). This is the first study to demonstrate that individual cheetahs, or any carnivores, may respond differently to a non-LGD and LGD breed.

Only two individuals – Mbili and Entito – moved following the VD playback, one moving away from the speaker and the other moving toward it, resulting in mixed interpretations of how they perceived VD presence. However, closer examination of their responses suggests neither provides evidence supporting either hypothesis. Mbili moved away from the speaker after VDs but did not move following LGDs or hornbills (Figure 2-2), initially suggesting he was only deterred by VDs. However, his movement was delayed (>20min after playback initiation) and brief. Additionally, he was less vigilant after VDs than after LGDs or hornbills (Figure 2-4). Thus, we infer his movement was more likely only a minor adjustment in position rather than a deliberate response to VDs.

Entito's response was more complex. She remained stationary after LGDs and hornbills but moved toward the speaker relatively soon after VDs (latency = 3:32). However, before moving, she detected an impala in the direction of, but well beyond, the speaker (>150m). As she moved, she passed within five meters of the speaker without showing awareness of it, eventually chasing and successfully killing the impala out of view. Thus, while the playback may have prompted initial arousal, it is difficult to attribute her subsequent behaviors to it alone. It is possible she perceived VDs as beneficial, either as prey, as a cue for livestock, or because dogs might displace herbivores like impala, improving hunting opportunities. Unlike other carnivores [43, 84], we are unaware of any confirmed instances of cheetahs killing dogs. Therefore, the latter explanation seems more plausible, especially considering the possibility of the playback arousing both her and the impala, improving her chances of detecting it in the speaker's direction. However, the impala's location may have been coincidental as we did not observe it before the playback. While further observations are needed to determine whether cheetahs perceive VDs as beneficial, this isolated observation makes one inference clear: VDs did not deter Entito nor dissuade her from hunting in the direction of the speaker, suggesting she perceived little, if any, threat from their presence.

The other seven cheetahs did not exhibit a strong response to VDs beyond a brief increase in vigilance toward the speaker during the first five minutes (Figure 2-3), a pattern also observed when comparing the responses of the six individuals exposed to the hornbill playback (excluding NMC). Also, only four individuals increased their activity during this period, while the other three remained inactive (Figure 2-3). One study found cheetahs may combine vigilance with activity when searching for prey [55], and used vigilance while prone to detect approaching threats [55], suggesting different individuals potentially perceived VDs differently. Nevertheless, given that more than half of the seven individuals returned to baseline levels of both vigilance and activity during their observation periods (Figure 2-4), their longer-term responses suggest that the presence of VDs had only a minimal and short-term behavioral effect, regardless of initial perceptions.

Our findings that VDs are unlikely to deter or attract cheetahs contrast with the evidence of deterrence observed with LGDs. However, this aligns with another study that found little behavioral response in pumas to audio playbacks of barks from non-LGD breeds [47]. Cheetahs may not have perceived VDs as a significant threat due to their smaller size than LGDs. Although cheetahs could not visually assess the size of the dogs during our study, they might have inferred this from the distinct acoustic characteristics of their barks or through prior experiences with VD sizes and their vocalizations. While cheetahs are known to avoid larger carnivores, such as lions and hyenas, there is limited data on how they respond to smaller, subordinate carnivores and mesocarnivores. However, numerous observations by the lead author suggest that cheetahs are not particularly wary of black-backed jackals (*Canis mesomelas*). In several instances, he even observed cheetah cubs chasing jackals away from kills. Our experimental reactions are consistent with cheetahs perceiving VDs as non-threatening as jackals.

Our LGD and VD playbacks differed in novelty, volume, and frequency, which is a reliable indicator of size in mammals. Thus, we attribute the main difference in reaction to the two breeds reflected simple perceived risk of bodily injury from LGDs. The large size of LGDs is probably advantageous for such warning vocalizations and their fighting capabilities if encounters with wildlife escalate. Notably, the differing reactions to LGDs and non-LGD breeds tend to rule out that fear of dogs is related to either dog breed’s association with humans. If that were the case, similar responses would be expected for both types of dogs, suggesting instead that cheetahs respond to specific characteristics of their vocalizations rather than their perceived connection to humans.

Broader Implications: Our findings that LGDs can deter individual cheetahs carry significant implications for cheetah ecology in areas shared with humans and their domestic animals. The short-term deterrence observed in five individuals suggests that LGD vocalizations can displace cheetahs from interaction locations. The longer-term impacts of such deterrence depend on its duration and severity (i.e., how far individuals are displaced and for how long). Prolonged displacement, lasting hours or even days, could lead to local extirpation from areas where LGDs frequently occur. For example, Ordiz et al. (2013) found that brown bears (*Ursus arctos*) avoided human interaction sites for multiple days following encounters [85]. If LGDs elicit similar long-term avoidance in cheetahs, their consistent presence could effectively exclude cheetahs from these regions, particularly if individuals reencounter LGDs before the initial effect subsides. Although our study did not measure the duration or extent of deterrence, this possibility cannot be dismissed. Future research should prioritize assessing how far and for how long cheetahs may be displaced following interactions with LGDs.

Despite the above implications, our observations of more cheetahs remaining stationary in response to LGDs suggest that vocalizations alone are unlikely to displace all individuals. This indicates that even among those deterred, displacement may be short-lived (lasting seconds to hours) and minimally severe. Theoretically, this should allow for coexistence between cheetahs and LGDs, at least within the auditory range. Cheetahs may be particularly well-adapted to coexist with LGDs, even if perceived as potential threats, as they have evolved to live alongside larger carnivores, such as lions and hyenas, by employing short-term avoidance rather than long-term displacement [51, 56, 71, 86]. This is further supported by a previous study using camera traps on farms that employ the same LGD breed used in our playbacks, which found similar cheetah occupancy on farms with and without LGDs [29]. However, our study did not account for additional variables that could influence the duration and severity of deterrence. For example, cheetah-specific factors such as sex, reproductive status (e.g., females with or without cubs), or social structure (e.g., solitary males versus coalitions) may affect how far or how long individuals are displaced. Similarly, LGD-specific factors may influence deterrence, including the number of dogs, their sexes, individual personalities, husbandry practices, and breeds. Many of these variables have demonstrated varying effectiveness in livestock protection [36, 87-89]. Therefore, future research should explore how these factors impact deterrence, as they may have significant implications for specific groups within cheetah populations.

The responses of cheetahs that did not move following the LGD playback, along with the lack of movement from most cheetahs after the VD playback, suggest that the presence of these dogs may have little direct effect on individual behavior. However, the presence of dogs, particularly LGDs due to their larger size, may still result in direct and indirect effects that negatively impact cheetahs. First, even without displacing cheetahs, LGDs may pose a risk to their safety and survival. Although LGDs are commonly present in cheetah habitats, particularly in Namibia and South Africa [37-39, 50, 82], direct negative interactions are rarely documented. However, incidents such as an LGD killing a cheetah highlight the potential for conflict [28]. Second, dogs may compete with cheetahs for prey, as dietary overlap is significant (e.g., Thomson's gazelle or hare) [31, 35, 44, 90]. Finally, dogs may carry diseases that can affect cheetahs and other carnivores [44, 91-93]. These indirect effects of dogs underscore the need for optimal dog management around cheetahs and other carnivores.

Limitations: One concern is whether our audio playbacks elicited responses accurately reflecting how cheetahs would naturally behave during interactions with real LGDs, VDs, frogs, or hornbills. Cheetahs rely heavily on visual cues for detecting threats and prey [55, 86, 94, 95], suggesting the use of visual stimuli instead of audio, might have led to different results. However, the use of audio playbacks is supported by numerous studies on wild large carnivores, including cheetahs, to infer deterrence and attraction [47, 57-59, 68-71, 96].

Our study also faced challenges related to sample size and study conditions. Although our sample size was modest (15 cheetahs), we had few subjects in coalitions or that had recently dispersed from their mother, which limited our ability to draw inferences about potential variations in response to each dog breed. For example, we conducted only 12 of 40 trials on six males and three of 40 on two recently dispersed individuals. The larger size of male cheetahs might lead them to perceive certain breeds of dogs as less threatening, while recently dispersed cheetahs might be extra cautious due to their inexperience.

Additionally, direct observations from a vehicle may introduce biases, as the vehicle's presence could influence how cheetahs perceive human-associated stimuli. This is particularly relevant in the Maasai Mara, where herders often avoid stopped vehicles to prevent disturbing tourist encounters with cheetahs, potentially leading cheetahs to associate the presence of any human-associated stimuli as less threatening when vehicles are nearby. Lastly, vehicle-based observation limited our trials to specific habitats and daylight hours. Cheetahs might feel more secure and less conspicuous in dense habitats where we could not conduct trials, leading to varying responses. In addition, cheetahs frequently move and hunt at night [97, 98], suggesting interactions with dogs might occur at different times of day. Dogs or cheetahs might be more aggressive at night, or cheetah more cautious at night if fleeing from a dog increases their conspicuousness to other carnivores who are more active at night. Future research could test other methods able to observe short-term behavior during interactions between cheetahs and dogs in various habitats for times of day, such as high-resolution collared cheetahs and dogs or using thermal cameras [45, 46]. Such research would further elucidate how cheetahs respond to dogs in various conditions.

Conservation Recommendations: Our results provide the first direct evidence that LGDs can deter individual cheetahs, reinforcing the assumption that LGDs directly protect livestock from predation. However, this finding has two important limitations influencing their role in cheetah conservation. First, while some cheetahs moved away from the speaker after the LGD playback most remained stationary, indicating that LGDs may not deter all individuals. This variation suggests that while certain cheetahs may avoid livestock herds protected by LGDs, others could continue to cause conflict. Therefore, in cases where LGDs significantly reduce or eliminate livestock predation, such effectiveness might stem from a combination of LGD directly deterring cheetahs and other indirect effects of their presence, such as alerting herders to the presence of cheetahs, who can then intervene. Conversely, if predation continues despite LGD presence, it would signal the need for additional non-lethal methods to complement LGDs and deter individual cheetahs that may still pose a threat.

Second, for those cheetahs that are deterred by LGDs, there is limited data on the duration and severity of the deterrent effect. Long-term or severe deterrence could result in cheetahs being displaced, potentially leading to unintended negative consequences for their populations. Thus, the placement and use of LGDs should account for these possibilities until further research determines whether LGDs are likely to cause displacement and how their presence can be managed to mitigate this effect. For example, limiting the number of LGDs deployed with livestock herds might reduce the frequency of deterrent effects, lowering the risk of long-term displacement. Alternatively, using playbacks of LGDs instead of actual LGDs might be easier to implement and limit the deterrent effects. Despite this limitation, our observations and existing studies, including those showing equivalent cheetah occupancy in areas with and without LGDs [29], suggest that any deterrence caused by LGDs is likely short-term. Therefore, while further research should continue to explore the effects of LGDs on cheetah behavior, our results corroborate numerous studies that recommend their use as a valuable tool in protecting livestock and promoting the long-term coexistence of people and cheetahs [28, 29, 37-40, 49, 50, 82, 99, 100].

In contrast to LGDs, we found no evidence that the presence of VDs causes deterrence or attraction. This suggests that their presence is unlikely to significantly impact cheetah behavior or distribution. However, this does not mean that VDs do not need to be managed. The indirect effects of VD presence are likely to negatively impact cheetahs and other wildlife, particularly through competition for prey competition and the spreading of disease. For this reason, we recommend regulating VD presence populations, especially free-ranging feral populations. In specific contexts, however, VDs and other non-LGD breeds may be acceptable and lead to positive outcomes promoting coexistence. For example, vaccinated pet dogs that only accompany people into carnivore habitats during recreational activities are unlikely to cause significant adverse impacts. Additionally, VDs around settlements with livestock or accompanying livestock herds might help reduce predation not by directly deterring cheetahs but by alerting people who can then intervene.

Appendix 1: Habituation

We evaluated habituation by testing whether individuals exposed to three or more playbacks (n = 9; six total playbacks, including LGD, VD, and frog playbacks) exhibited decreasing changes in vigilance toward the speaker and activity during PPI 1 and or the entire PPP of each trial as they were exposed to more playbacks. Individuals exposed to three or fewer playbacks (n = 3) were excluded due to the increasing likelihood of habituation with greater exposure. To encompass the potential habituation to our method (e.g., speaker placement), we considered the total number of playbacks (including treatment and control playbacks) rather than just the treatment playbacks. We used Spearman's rank correlation rho tests to initially examine whether individual changes in either behavior during PPI 1 or the entire PPP decreased with increased exposure to more playbacks (Table 2-A1-1). Subsequently, we used one-sample Wilcoxon signed rank tests to determine whether the slope parameters for each behavior change during the two timescales statistically differed from zero, with negative slope parameters indicating reduced changes in behavior as individuals were exposed to more playbacks (Table 2-A1-2). We found no evidence of habituation.

Table 2-A1-1: Changes in vigilance and activity for individual cheetahs as they were exposed to an increasing number of playbacks.

Cheetah Name/Interval & Behavior Change	**1st Post-Playback Interval**						**Post-Playback Period**					
	Change in Vigilance			Change in Activity			Change in Vigilance			Post-Playback Period		
	rho =	S =	p =	rho =	S =	p =	**rho =**	**S =**	**p =**	**rho =**	**S =**	**p =**
Entito (n = 6)	-0.14	40	0.8	-0.13	39.58	0.8	-0.61	56.31	0.2	-0.52	53.26	0.23
Kuahidi (n = 6)	-0.37	48	0.5	-0.17	40.92	0.75	-0.03	36	1	-0.06	37.03	0.91
Kulete (n = 6)	0.43	20	0.42	-0.64	57.32	0.17	0.77	16	0.78	-0.71	60	0.14
Nebaati (n = 6)	0.6	14	0.24	0.21	27.56	0.69	-0.14	40	0.8	0.31	24	0.56
Mbili (n = 6)	0.03	33.99	0.96	-0.64	57.31	0.17	-0.03	36	1	-0.64	57.31	0.17
Neema (n = 5)	0.3	14	0.68	0.7	6	0.69	-0.3	26	0.68	-0.9	38	0.08
Selenkei (n = 5)	0.3	14	0.68	0.11	17.76	0.86	0.41	11.79	0.49	0.2	16	0.78
Sila (n = 5)	0.3	14	0.68	-0.1	22.1	0.87	0.3	14	0.68	-0.3	26	0.68
Leteipa (n = 5)	0.6	8	0.35	0.67	6.58	0.22	0.2	16	0.78	0.67	6.58	0.22

Correlations were tested with Spearman's rank correlation rho tests.
n indicates the number of playbacks each individual was exposed to.

Table 2-A1-2: Habituation test examining whether the slope parameters of individual cheetahs differ from zero.

Interval & Behavior Change	**Median rho =**	**V =**	**p =**
1st Post-Playback Interval			
Change in Vigilance	0.3	37	0.1
Change in Activity	-0.1	24	0.91
Post-Playback Period			
Change in Vigilance	-0.03	25.5	0.77
Change in Activity	-0.3	13	0.3

Comparisons were completed with the Wilcoxon signed rank test.
The median rho value was calculated from the slope parameters for individual cheetahs in Appendix 1: Habituation - Table 2-A1-1.

Appendix 2: Order-Effects

Within-Subject Tests: For within-subject assessments of each treatment stimulus (LGD, VD), individuals exposed to both treatment and control stimuli (frog, hornbill) were divided into Treatment-First and Control-First groups based on which stimulus they were exposed to first, following the Hills-Armitage approach. While some cheetahs were exposed to other stimuli between the two stimuli, we hope our random sequence of stimuli and assessment of habituation raise confidence that intermediate exposures had minimal influence on responses. For each individual, we calculated the difference in change in vigilance toward the speaker and activity during PPI 1 and the entire PPP following exposure to the treatment and control stimuli (treatment – control). We then used a two-sample Wilcoxon rank sum test to compare the difference in median change for both behaviors between Treatment-First and Control-First individuals (Table 2-A2-1). We found no statistical difference in either behavior during any period, suggesting no order effect (Table 2-A2-1).

Table 2-A2-1: Within-subject subject tests comparing median changes in percent time active and vigilant toward the speaker among individual cheetahs who received a treatment playback before the control and individuals who received the control playback before treatment, and between individuals who received the cattle playback before the shoat and individuals who received the shoat playback before the cattle.

LGD vs. Frog	LGD-First (n = 3)	Frog-First (n = 4)	W =	p =
Vigilance Toward the Speaker	Median Difference (IQR)	Median Difference (IQR)		
1st Post-Playback Interval	+52%% (+49 to +74)	% (% to %)	10	0.23
Post-Playback Period	+32%% (% to %)	% (% to %)	8	0.63
Change in Activity	Median Difference (IQR)	Median Difference (IQR)		
1st Post-Playback Interval	+81% (+41 to +88)	+82% (+57 to +90)	5.5	1
Post-Playback Period	+61% (+31 to +80)	+17% (-4 to +47)	8.5	0.48
VD vs. Hornbill	VD-First (n = 2)	Hornbill-First (n = 6)	W =	p =
Vigilance Toward the Speaker	Median Difference (IQR)	Median Difference (IQR)		
1st Post-Playback Interval	+21% (+13 to +29)	+11% (+3 to +25%)	8	0.64
Post-Playback Period	0 % (-7 to +6)	-1% (-7 to +10)	6	1
Change in Activity	Median Difference (IQR)	Median Difference (IQR)		
1st Post-Playback Interval	+39% (+20 to +58)	+13% (0 to +48)	9	0.40
Post-Playback Period	+9% (+6 to +13)	+5% (0 to +11)	8	0.64
LGD vs. VD	LGD-First (n = 2)	VD-First (n = 6)	W =	p =
Vigilance Toward the Speaker	Median Difference (IQR)	Median Difference (IQR)		
1st Post-Playback Interval	+30% (+3 to +57)	+5% (-12 to +13)	7	0.86
Post-Playback Period	+23% (-1 to +47)	+3% (-9 to +14)	7	0.87
Change in Activity	Median Difference (IQR)	Median Difference (IQR)		
1st Post-Playback Interval	+36% (+23 to +49)	-6% (-22 to +23)	10	0.29
Post-Playback Period	+15% (+2 to +28)	-5% (-11 to +5)	8	0.64

Comparisons were analyzed using the Hills-Armitage approach [74] and Wilcoxon rank sum test. Individuals receiving only one playback were excluded.

Between-subject comparisons were analyzed using the Wilcoxon rank sum test.

IQR refers to the interquartile range of the median difference, Q1 to Q3.

Appendix 3: Intercoder Reliability

We evaluated intercoder reliability across nine actual trial videos. Each coder, Brian Schuh (B.S.), Camilla Husted Steinfurth (C.H.S.), and Kim Preston (K.P.), independently coded three trial videos assigned to each of the other coders. We compared how each coder measured activity and vigilance toward the speaker. Measurement precision was assessed by calculating the average absolute difference between corresponding behavioral measures recorded by the two individuals across all nine videos. Our findings indicate an average measurement precision of 0.1% for activity and 1.5% for vigilance toward the speaker (Table 2-A3-1).

Table 2-A3-1: Intercoder reliability tests across nine actual trial videos.

Interobserver Reliability Test				
	B.S.	**C.H.S.**	**K.P.**	**Measurement Precision**
Video 1 (1:05:00 hr:min:sec)				
Vigilant Toward Speaker	17.9%	18.2%		0.3%
Active	3.5%	3.4%		0.1%
Video 2 (1:05:00, hr:min)				
Vigilant Toward Speaker	27.7%	25.6%		2.1%
Active	3.3%	3.3%		0.0%
Video 3 (1:05:00, hr:min:sec)				
Vigilant Toward Speaker	10.3%	10.2%		0.1%
Active	1.6%	1.6%		0.0%
Video 4 (0:12:48, hr:min:sec)				
Vigilant Toward Speaker	24.3%		24.5%	0.2%
Active	59.6%		59.9%	0.3%
Video 5 (1:05:00, hr:min:sec)				
Vigilant Toward Speaker	19.6%		18.3%	1.3%
Active	0.0%		0.0%	0.0%
Video 6 (0:49:08, hr:min:sec)				
Vigilant Toward Speaker	10.2%		12.7%	2.5%
Active	0.0%		0.0%	0.0%
Video 7 (0:22:15, hr:min:sec)				

Vigilant Toward Speaker		16.0%	16.2%	0.2%
Active		17.9%	17.6%	0.3%
Video 8 (0:43:28, hr:min:sec)				
Vigilant Toward Speaker		22.1%	20.7%	1.4%
Active		0.0%	0.0%	0.0%
Video 9 (1:05:00, hr:min:sec)				
Vigilant Toward Speaker		23.5%	28.6%	5.1%
Active		0.8%	0.8%	0.0%
Average Measurement Precision - Vigilant Toward Speaker				1.5%
Average Measurement Precision - Active				0.1%

B.S. indicates coder Brian Schuh
C.H.S. indicates coder Camilla Husted Steinfurth
K.P. indicates coder Kim Preston

Appendix 4: Playback Decibels

Table 2-A4-1: Observed and achieved playback decibels.

Playback	Exemplar	Observed (dB)	Achieved (dB)
LGD	1	64	61.3
	2		63.8
	3		59.6
VD	1	58	57.7
	2		56.2
	3		56.6
Frog	1	44	42.4
	2		42.8
	3		42.8
Hornbill	1	54	55.3
	2		53.7
	3		52.9

Observed decibels were recorded from 40m of livestock guarding dogs (LGDs), village dogs (VDs), or from wild hornbills and frogs.

Achieved decibels were measured from 40m away from the playback speaker.

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Chapter 3: Examining Correlations Between Humans' Attitudes towards Carnivores and their Accuracy of Species Identification

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Abstract. People with negative attitudes toward carnivores may kill them, potentially threatening many populations. In communities coexisting with multiple species, each carnivore is likely associated with distinct costs and benefits, such as differing risks to livestock or contributions to wildlife tourism, which may shape species-specific attitudes. Alternatively, individuals might generalize their attitudes across species. One factor potentially influencing whether individuals hold species-specific or generalized attitudes is their ability to identify each species. Misidentification might lead to misapplied perceptions of costs and benefits, resulting in similar attitudes toward confused species. Despite acknowledging this possibility, few studies have explored the relationship between identification ability and species-specific perceptions. Here, we surveyed 283 community members near Kenya's Maasai Mara National Reserve to assess their perceptions about, and ability to identify, six carnivore species (cheetahs, lions, leopards, African wild dogs, spotted hyenas, and striped hyenas). Using within-subject analysis, we tested three sets of hypotheses to examine whether respondents hold species-specific or generalized perceptions (H1), whether identification ability correlates with perceptions (H2), and whether misapplied perceptions arise from misidentification (H3). We found strong support for species-specific perceptions across most species, with weaker evidence between lions and African wild dogs. Identification ability was associated with perceptions of leopards, spotted hyenas, and African wild dogs but not cheetahs, lions, or striped hyenas. Misapplied perceptions were not strongly supported. However, limited evidence suggests respondents who confused spotted hyenas with cheetahs may have misapplied positive perceptions of cheetahs onto spotted hyenas, and those who confused African wild dogs with spotted hyenas may have misapplied negative perceptions of spotted hyenas onto African wild dogs. These findings indicate that

respondents perceive distinct costs and benefits from different species, likely contributing to variations in attitudes and behaviors. This underscores the importance of measuring species-specific attitudes, as both the risk of anthropogenic mortality and the effectiveness of management interventions will likely vary by species. Furthermore, assessments of identification ability should be measured for a wider range of species, as misidentification may shape attitudes toward certain wildlife, especially among respondents prone to species confusion.

Introduction

Anthropogenic mortality of carnivores, often in response to perceived or actual threats to livestock or personal safety, significantly contributes to the decline and local extirpation of many populations [1-6]. Identifying individuals who kill carnivores is challenging, as some may act illegally and conceal evidence [7, 8]. Despite some limitations [9, 10], individual attitudes toward carnivores can reflect underlying wildlife values that may influence behavior [11-13]. Consequently, researchers who measure attitudes aim to predict behaviors by increasing our understanding of the characteristics of those more likely to kill carnivores, fostering coexistence by reducing anthropogenic mortality.

Attitudes are frequently linked to perceptions of the economic, social, and cultural costs and benefits associated with carnivores. For example, economic and cultural costs of livestock predation commonly correlate with more negative attitudes [10, 14-22], while economic benefits, such as associating carnivores with ecotourism or government subsidies, are associated with more positive attitudes [16, 23, 24]. Additionally, peer group identity and social norms (i.e., shared expectations within a community about appropriate behaviors) also seem to influence attitudes in social surveys. For example, in Brazil, a correlation was found between ranchers' willingness to kill carnivores and their belief that others in the community did so. However, few experimental studies examine attitudes toward carnivores, leaving causal mechanisms largely unknown. Notable exceptions include Pineda Guerrero (2023) and Slagle et al. (2013). Through experimental manipulation, Pineda Guerrero found that respondents' involvement in projects aimed at coexistence may be more potent than non-lethally deterring carnivores from attacking livestock [25]. Further, the results of experimentation by Slagle et al. (2013) suggest that perceived costs and benefits are important to a person's attitudes [26]. Therefore, it is likely that the field will continue to measure perceived costs and benefits to gain insights into behaviors that promote or undermine coexistence. However, few studies have measured attitudes toward multiple carnivore species coexisting within the same landscape.

Although many studies examine individual perceptions of costs and benefits associated with carnivores, most focus on a single species or consider carnivores as a group without specifying interspecific differences [10, 16, 23, 24, 27-32]. In communities coexisting with multiple carnivore species, however, each is likely associated with distinct costs and benefits or with varying degrees of similar ones, such as one species killing more livestock than another [18, 20, 32-37]. If individuals perceive these differences, they may develop species-specific attitudes and behaviors, leading to different levels of anthropogenic mortality across species. Consequently, people from varying socioeconomic backgrounds may be more inclined to kill certain species over others, indicating the need for tailored management interventions to address specific costs and benefits for each. Alternatively, individuals may rely on cognitive shortcuts and develop generalized perceptions, such as viewing all carnivores as threats, which may lead to generalized attitudes and behaviors toward multiple species [6, 38]. In this case, predictions about anthropogenic mortality risk, the socioeconomic characteristics of people more likely to kill carnivores, and the appropriate management interventions could be generalized to other regions, species, or coexistence systems, in principle.

However, only a few studies have investigated whether individual perceptions vary by species [15, 32, 36-39]. Those that have primarily examined perceived differences in the risks each species poses to livestock, providing evidence for both species-specific and generalized perceptions. For example, Mkonyi et al. (2017) reported significant variation in the number of respondents who ranked cheetahs (*Acinonyx jubatus*), lions (*Panthera leo*), leopards (*Panthera pardus*), African wild dogs (*Lycaon pictus*), and spotted hyenas (*Crocuta crocuta*) as major problems. Conversely, Dickman et al. (2014) found that respondents who viewed one of the same five carnivore species as problematic were more likely to perceive all species as problematic. Therefore, in communities with multiple carnivore species, further studies are needed to understand how individuals perceive the distinct costs and benefits associated with each. Such knowledge could enhance predictions of mortality risk and guide the development of more effective, species-specific management interventions.

A prerequisite to species-specific attitudes and behaviors is the ability to distinguish species under wild conditions. Without this ability, individuals may develop misapplied perceptions, where perceptions about one species are incorrectly attributed to another that they confuse it with. For example, if individuals perceive higher costs from species A but confuse species B for A, they may attribute those costs to B, leading to similarly negative attitudes and an increased mortality risk for both species. Conversely, if they perceive greater benefits from species A but confuse species B with A, they may attribute those benefits to B, resulting in more positive attitudes and a reduced mortality risk for both species, even if they might otherwise be more likely to kill B. Depending on which occurs, misapplied perceptions could suggest that species-specific management interventions may be inefficient, as actions tailored for one species might be inappropriately generalized to others. This confusion may lead to strategies that fail to address each species' specific costs or benefits, undermining efforts to reduce mortality risk or promote coexistence effectively. Multiple studies have acknowledged the possibility of misapplied perceptions when examining attitudes about similar-looking species' threats to livestock, such as cheetahs and leopards [15, 40, 41]. However, few have explored the relationship between identification ability and individual perceptions. The research gaps described above make it challenging to determine whether confusion over species leads to misleading data and mistimed or poorly designed interventions.

Here, we conduct a survey to examine whether individuals in the community surrounding the Maasai Mara National Reserve hold species-specific perceptions about four expected costs and benefits associated with six native carnivore species: cheetahs, lions, leopards, African wild dogs, spotted hyenas, and striped hyenas (*Hyaena hyaena*). In addition, we investigated whether individual abilities to identify each species correlate with their perceptions about it and, if so, whether they may be misapplying perceptions from one species to another. By evaluating perceptions alongside species identification abilities, we aim to understand better whether individuals hold species-specific, generalized, or misapplied perceptions. We anticipate improvements in our ability to predict the risk of anthropogenic mortality for each species and the need for species-specific interventions.

We test three sets of contrasting hypotheses. The first set (H1) uses within-subject analysis to examine whether individuals hold species-specific or generalized perceptions about one species relative to the others. *Species-Specific Perceptions* predicts distinct perceptions for a particular species, while *Generalized Perceptions* predicts similar perceptions across two or more species. If *Species-Specific Perceptions* are supported, we infer that these distinct perceptions may predict unique attitudes and behaviors toward that species. If *Generalized Perceptions* are supported, we infer that similar perceptions may foster similar attitudes and behaviors across the relevant species.

Next, we test our second set of hypotheses for each species (H2), which examines whether individuals' ability to identify a species correctly correlates with their perceptions of it. We test H2 for all species, independent of the H1 findings. Support for *Species-Specific Perceptions* in H1 does not rule out the possibility that some individuals may still confuse that species with another, potentially leading them to hold similar perceptions about both. Similarly, support for *Generalized Perceptions* in H1 could suggest that individuals generalize their perceptions due to an inability to distinguish between species, indicating that identification ability may influence perception generalization.

H2: *ID Does Not Correlate with Perceptions* predicts that respondents who correctly identify a species hold similar perceptions to those who misidentified it. In contrast, *ID Correlates with Perceptions* predicts that respondents who correctly identify a species hold different perceptions than those who misidentified it. If *ID Does Not Correlate with Perceptions* is supported, we infer that an individual's ability to identify a species would not predict their perceptions. Additionally, if this hypothesis is supported for multiple species supporting *Generalized Perceptions* in H1, we would infer that individuals generalize their perceptions across species. If ID *Correlates with Perceptions* is supported, we would infer that identification ability correlates with individual perceptions, prompting us to test our third set of hypotheses (H3) for that species.

Our third set of hypotheses (H3) evaluates whether the ability to identify a species (A) was associated with different perceptions about it because those who misidentified it confused it with another species (B). *Misapplied Perceptions* predicts respondents' inability to identify species A is positively associated with their perceptions of the species they confused it with (species B; their perceptions about A are similar to their perceptions about B). *Diverging Perceptions* predicts respondents' inability to is negatively associated with their perceptions about the species they confused with it (species B; their perceptions about A are different than their perceptions about B).

If *Misapplied Perceptions* is supported, we would infer that individual attitudes and behaviors toward species A may be similar to those toward species B. This could manifest as artificially positive attitudes, where greater perceived benefits of B elevate perceptions of A, or artificially negative attitudes, where greater negative perceptions of B lower perceptions of A. Artificially positive attitudes might predict a reduced mortality risk for both species, even if species A is actually associated with greater net benefits. Conversely, artificially negative attitudes might predict an increased mortality risk for both species, even if species A is actually associated with lower net benefits.

If *Diverging Perceptions* is supported, we would infer that attitudes and behaviors toward both species will likely differ, even when individuals confuse them. However, the inability to identify species A could still predict distinct attitudes and behaviors toward it compared to those who correctly identified it. For example, difficulty in identifying a species has been associated with lower attitudes toward it [15]. Therefore, if individuals who struggle to identify species A report lower perceived net benefits, this may suggest a greater likelihood of negative behaviors toward it. Consequently, targeted educational programs to improve species identification may foster more positive attitudes without necessitating additional interventions to address the actual costs or benefits associated with species A.

Here, we examine how individuals living alongside multiple carnivore species perceive the costs and benefits of each and how their ability to distinguish between them correlates with those perceptions. Addressing this gap in our understanding may help to protect imperiled carnivores facing ongoing declines in human-dominated ecosystems. A nuanced understanding of how individual perceptions about multiple carnivore species are influenced will enable more accurate predictions about each species' risk of anthropogenic mortality and the need for tailored management interventions that effectively address each species' specific costs and benefits. These insights could ultimately foster coexistence and reduce the risk of human-carnivore conflict.

Methods

Study Site:

Our study is conducted in Kenya's Maasai Mara, located on the southwest border with Tanzania. This region includes two types of protected landscapes: the Maasai Mara National Reserve (MMNR), managed by the Narok County Government, and privately owned wildlife conservancies (Figure 3-1). Human settlements are primarily concentrated along the peripheries of these protected areas, though a small number of permanent residents also inhabit the conservancies.

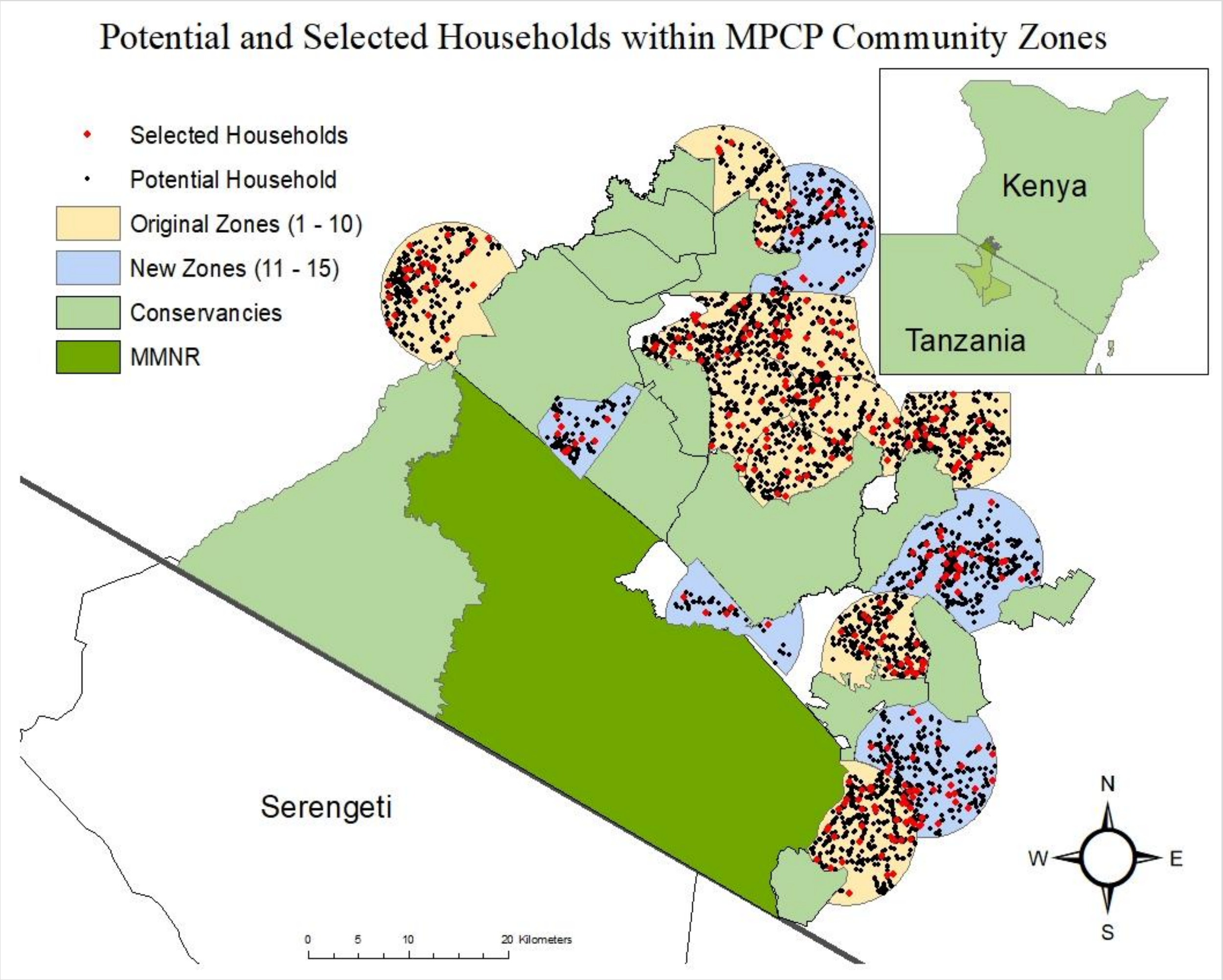


Figure 3-1: Kenya's Maasai Mara National Reserve (MMNR; dark green) and surrounding wildlife conservancies (light green). Zones are primarily located outside the MMNR and wildlife conservancies, but some overlap with conservancy land. The Mara Predator Conservation Programme (MPCP) designated ten original zones (light yellow) in June 2020 and five new zones (light blue) in July 2021. White areas internal to the map represent unprotected community land not included in a zone. 300 households (red dots) were selected from the 3,890 (black dots) in the fifteen zones. MPCP created and permitted me to publish this map.

Survey Design:

The Mara Predator Conservation Programme (MPCP) surveyed residents in fifteen different zones along the peripheries of the MMNR and conservancies. MPCP has extensive experience conducting surveys and outreach programs within the surrounding community [23, 42, 43]. MPCP's Programme Manager, Michael Kaelo (MK), developed the survey instrument with the help of the authors. Fifteen MPCP employees, referred to as Lion Ambassadors (LAs), were trained to administer the questionnaires. LAs play an integral role in the community, recording household locations, livestock predation incidents, and the carnivore species perceived as responsible within their assigned zone. MPCP established ten zones in June 2020 and added five more in July 2021 (Figure 3-1).

Administering this survey within the established zones offered several advantages. First, utilizing LAs as interviewers, who are community members themselves, likely enhanced respondents' willingness to provide truthful answers and reduced refusals. This is supported by previous MPCP surveys, which also used local interviewers (including some of the same LAs) and reported a 100% response rate [23, 43]. Second, the staggered establishment of zones (ten in June 2020 and five more in July 2021) allowed for comparisons between respondents, potentially allowing us to identify if the duration of LA presence correlates with perceptions toward each species. This is relevant given previous findings suggesting reduced lion killings when community members in the Maasai Mara were employed to warn others of lion presence, a role similar to LAs [44].

Despite these advantages, our zone-based sampling approach, dictated by field logistics and time constraints, also imposes limitations. While randomization within the sampling frame minimizes self-selection bias, it excludes households outside the zones, potentially introducing bias if LA presence influences perceptions. Additionally, the LAs’ relationships with fellow community members might affect the interview processes in ways we could not control. For example, respondents were likely aware of the LAs’ affiliation with MPCP, which could have influenced their answers to align with perceived expectations.

Sampling:

We randomly selected 300 households across 15 zones (Figure 3-1), representing 7.71% of the 3,890 identified households. The number of households selected per zone ranged from 5 to 43, with an average of 20 per zone. This sample size was chosen based on previous MPCP survey efforts [43], balancing the time required for Lion Ambassadors (LAs) to conduct surveys with the need to detect sufficient errors in species identification for robust statistical analysis. Each LA was responsible for conducting one interview with the eldest male at each selected household within their assigned zone. This approach was informed by the understanding that senior males typically own the household's livestock and land, including any land leased to conservancies [23].

Survey Questions and Instrument:

MPCP designed the survey instrument based on a previous questionnaire [23, 43], expanding its focus from general attitudes and behavioral intentions toward carnivores as a collective to measuring perceptions about six native species in the Maasai Mara: cheetahs, leopards, lions, African wild dogs (AWDs), spotted hyenas, and striped hyenas. The instrument includes three sections: background, species identification, and species-specific perceptions.

Background: This section, taken directly from MPCP's previous survey instrument [23], collects data on respondents' age, education, occupation, religion, and land ownership within specific conservancies (Appendix 4: Survey Instrument – Background).

Species Identification: Adapting the methodology of Madsen et al. [43] and similar studies, we used three photos for each species, instead of a single photo, to provide a more comprehensive assessment of species identification ability. The photos depicted individuals in three distinct postures to reflect how respondents might encounter wild individuals: walking (flank view), walking head-on (toward the camera), and lying down (lying on their flank with their four legs coming towards the viewer and their head touching the ground) (Figure 3-2; Appendix 4: Survey Instrument - Species Identification: 1). Each photo randomly depicted either a male or female, with efforts made to include at least one of each sex for each species, except for lions (where only females were used due to males' distinctive appearance [23]) and striped hyenas (where sex was unknown due to limited image availability). Most of the photos were taken in the Maasai Mara by the lead author, but some were collected through social media (after the owner gave consent). During each interview, LAs haphazardly presented (procedure described below) each of the 18 carnivore photos one at a time to the respondent and asked, “What animal do you see in this photo?” (Appendix 4: Survey Instrument – Species Identification 2).

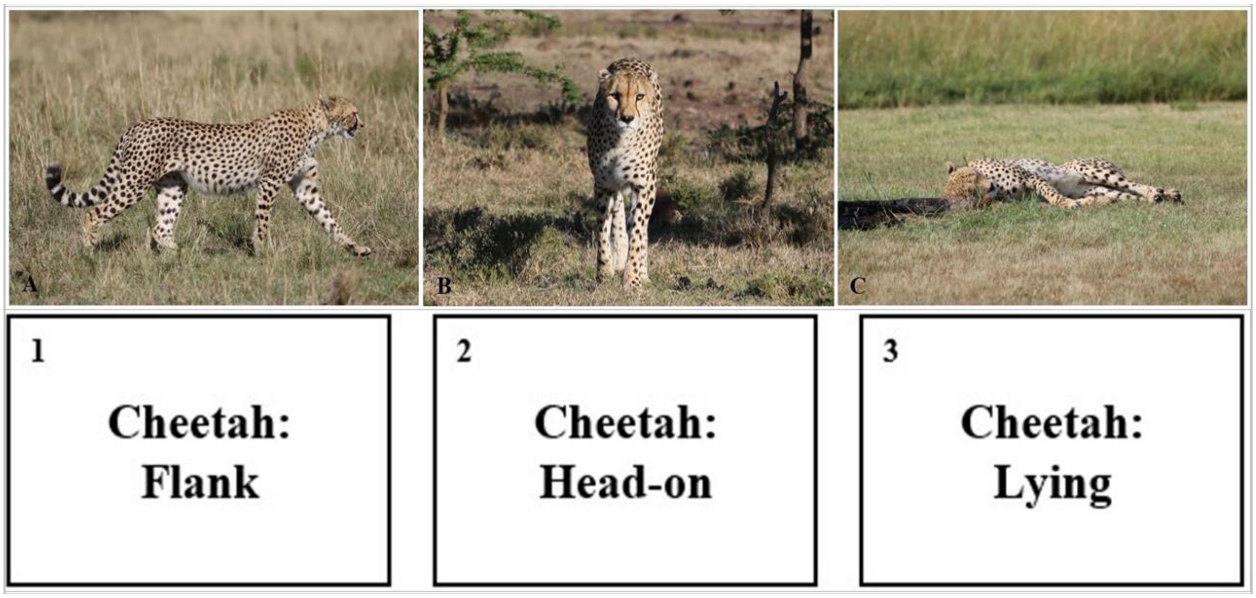


Figure 3-2: The three cheetah photos presented to respondents during each interview (top). Photos of the other five species, leopard, lion, African wild dog, spotted hyena, and striped hyena, fit the same body posture criteria. A: cheetah Flank, B: cheetah walking head-on, C: cheetah lying down. Three cards from Set 1 correspond to the three cheetah photos (bottom). Set 1 had 18 cards, each corresponding to a single photo. Three similar cards were made for each of the other five species.

Species-Specific Perceptions: To measure respondents' perceptions of each carnivore species, MK and the lead authors developed eight statements, four focusing on potential benefits and four on potential costs commonly associated with carnivores (Appendix 4: Survey Instrument – Species-Specific Perceptions: 1):

Benefit Statements (BS):

- BS1: *"I think seeing [species name] is enjoyable."*
- BS2: *"I think [species name] are important to tourism."*
- BS3: *"I think [species name] are important to me and my family's employment or income."*
- BS4: *"I think [species name] play an important role in maintaining a healthy ecosystem."*

Cost Statements (CS):

- CS1: *"I think [species name] pose a significant risk to my livestock."*
- CS2: *"I think [species name] pose a significant risk to other people's livestock."*
- CS3: *"I think [species name] pose a significant risk to me or my family."*
- CS4: *"I think [species name] pose a significant risk to other people in the community."*

Respondents were asked to indicate their level of agreement with each statement on a five-point Likert scale (strongly disagree, disagree, neutral, agree, strongly agree) [27, 45, 46]. Respondents could provide their answers verbally or by pointing to a visual cue (Figure 3-3). The visual cue consisted of five faces, each corresponding to a potential answer in the Likert scale. For benefit statements, the scale ranged from a big smiley face corresponding with strongly agree to a big frowny face corresponding with strongly disagree (Figure 3-3). For cost statements, the scale was reversed, with the big smiley face corresponding with strongly disagree and the big frowny face corresponding with strongly agree (Figure 3-3). Black and white faces were chosen to avoid potential misinterpretations related to cultural associations with color or color blindness.

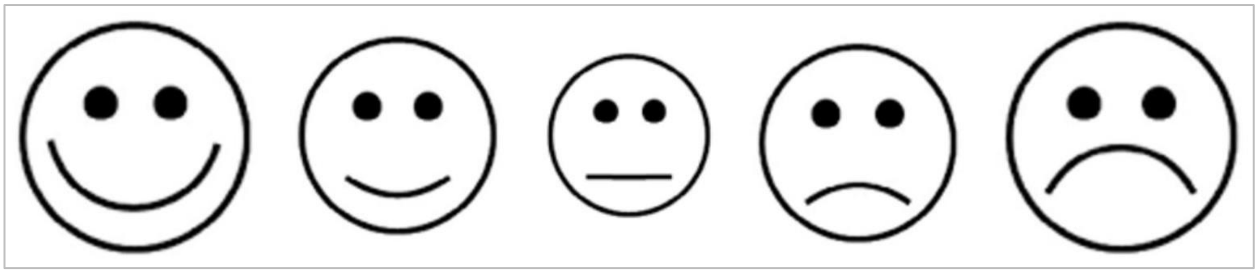


Figure 3-3: The face scale displayed for each respondent during the species-specific perceptions section of the survey. Respondents would point to the face corresponding to their answer to each of the eight statements. Benefits statements corresponded to the following faces: Strongly agree = big smiley face to Strongly disagree = big frowny face. Cost statements corresponded to the opposite faces: Strongly agree = big frowny face, to Strongly agree = big smiley face.

Lion Ambassador Training:

Before conducting interviews, MK, in collaboration with the lead authors, conducted a comprehensive one-and-a-half-day training session with all 15 LAs. Training began with a focus on species identification. LAs were tested on their ability to correctly identify the six focal carnivore species using 18 photos of carnivores in the survey instrument (three photos per species). An initial assessment revealed varying levels of proficiency: four LAs correctly identified all 18 photos, four identified 17, two identified 16, one identified 15, one identified 14, one identified 13, one identified 12, and one identified 10. Following a group review and discussion of each photograph, LAs were re-tested at the end of the first training day using the same photos in a new randomized order. The second assessment demonstrated improved performance: seven LAs correctly identified all 18 photos, four identified 17, two identified 16, one identified 14, and one identified nine. Any remaining misidentifications were individually reviewed and addressed with the respective LA. The data from the one LA that only correctly identified nine photos were ultimately excluded from the analysis (described in more detail below). The training covered key topics between species identification assessments, including the research objectives, research ethics, recruitment procedures, obtaining informed consent, and confidentiality protocols. On the second day, additional training reinforced these concepts. MK translated each survey question into Maa, the predominant language of the community, and led a group discussion to ensure all LAs fully understood and agreed upon the meaning of each question. The translation process was iterative, with revisions made until a consensus was reached regarding the intention of each question. Procedures for probing incomplete or inadequate responses were also discussed. MK and the lead author facilitated mock interviews with LA pairs to familiarize them with the interview protocol (described below). LAs alternated roles as interviewer and respondent during the practice sessions. On the second training day, LAs conducted a second round of mock interviews with new partners. Their performance was evaluated during each practice session, with feedback provided to address any errors or inconsistencies. Upon completion of training, each LA was provided with a smartphone preloaded with GPS coordinates for the selected households within their zone (Figure 3-1).

Interview Protocol:

LAs used GPS navigation on their MPCP-provided smartphones to locate each selected household based on preloaded coordinates. If a household was not present at the provided coordinates, LAs were instructed to conduct an interview at the nearest visible household.

Before initiating an interview, LAs introduced themselves and requested to speak with the eldest male of the household. If the eldest male was unavailable, LAs arranged to return at a more convenient time. If the eldest male was available, LAs explained the purpose of the survey, emphasizing its independence from government or management entities and clarifying that no compensation was provided for participation or for livestock losses. This step was intended to minimize any potential incentive for respondents to exaggerate the perceived threat of carnivores to their livestock. LAs also detailed the consent procedures, ensuring transparency about the study and the respondents' rights. This included assurances of respondents' privacy and confidentiality, their right to withdraw from the survey at any time without penalty, their right to abstain from answering any questions, and notification that the GPS location of the interview would be recorded. These measures aimed to build trust, avoid misrepresenting the survey's intent and reduce the likelihood of respondents providing dishonest answers due to misinterpretation of the survey's purpose.

Interview: LAs conducted interviews using a mobile phone application called Cybertracker®. The app was preprogrammed to replicate the written survey instrument (Appendix 4: Survey Instrument), guiding LAs through each question in the specified order. Forced-choice questions provided predefined response options, while open-ended questions allowed LAs to select from common answers or manually type unique responses.

As many individuals within the sampling frame may not know how to write, no signature was collected for consent. Instead, written signatures were not collected for consent. Instead, LAs requested oral consent, recording respondents' answers as either 'Yes' or 'No' within the Cybertracker®. If consent was denied, LAs expressed their thanks and proceeded to the next selected household. If consent was granted, LAs began with the background section of the survey instrument.

LAs presented each question from the background section of the survey instrument and recorded respondents' answers using Cybertracker®. After completing this section, LAs proceeded to the species identification portion of the survey.

We printed the 18 carnivore photos, three of each species, on A4-sized paper and laminated them for durability (Appendix 4: Survey Instrument – Species Identification: 1). LAs haphazardly presented each photo to the respondent. Aiming for a randomized order of photo presentation, each LA was provided with a set of 18 smaller laminated cards (Set 1), with each card corresponding to one of the A4-sized photos (Figure 3-2; Appendix 4: Survey Instrument – Species Identification: 3). Each species was represented by three cards, one for each of the three distinct photos (Figure 3-2). During the interview, LAs blindly selected one card at a time from an opaque folder, presented the corresponding A4-sized photo to the respondent, asked them to identify the animal in the photo, and recorded their response using Cybertracker®. The used card was then set aside, and the process was repeated until all 18 cards had been drawn and all photos presented. After completing this section, LAs shuffled the 18 cards thoroughly, returned them to the folder, and moved on to the Species-Specific Perceptions section of the survey.

Before presenting the cost and benefit statements, LAs ensured respondents understood the Likert scale by clearly explaining each potential response option (e.g., strongly agree to strongly disagree) and discussing their meanings. Additionally, LAs introduced a visual cue consisting of five faces representing each Likert scale response (Figure 3-3), carefully explaining the meaning of each face and its corresponding scale value. Respondents could provide their answers verbally or by pointing to the face that most accurately represented their response.

LAs recited the eight cost and benefit statements for each of the six carnivore species, totaling 48 responses per respondent. They completed all eight statements for a single species before moving on to the next. To randomize the order of species presentation, LAs blindly selected a card from Set 1 (described above; Figure 3-2), verbally identified the species indicated on the card to the respondent, and displayed the corresponding large A4-sized flank photo. To randomize the order of statements for the selected species, LAs used a separate set of eight cards (Set 2), each corresponding to one of the cost or benefit statements (Appendix 4: Survey Instrument – Species-Specific Perceptions: 2). They blindly selected one card at a time from a second opaque folder, read the corresponding statement from their phone, recorded the respondent's answer, and set the card aside. This process continued until all eight statements for the species were presented. After completing the statements for one species, LAs shuffled the Set 2 cards and returned them to the folder. Then, they selected a new species by drawing another card from Set 1. If a species was selected multiple times from Set 1 (each species had three corresponding Set 1 cards), LAs continued to draw cards until a new species was chosen. Once they completed all statements for all six species, LAs returned the cards in both Sets to their respective folders. LAs ended the interview by thanking the respondent for their participation, and recording the GPS location of the interview on Cybertracker®

Data Collection:

Data collection involved two scheduled meetings with each LA, during which MPCP downloaded completed surveys onto the Cybertracker® desktop application for review. The first meeting took place one week after the training session to evaluate the quality of interviews and identify potential errors. Due to numerous data entry errors, the interviews conducted by one LA (who had also correctly identified only nine photos during the second species identification assessment) were discarded. The remaining interviews in that LA’s zone were reassigned to another LA with greater proficiency in conducting accurate interviews. The second meeting occurred one month after training to collect data from the remaining surveys. All LAs, except one, completed their assigned interviews within this period. A third meeting was scheduled with that LA to retrieve the final data after they completed their outstanding interviews.

Confidentiality:

MPCP implemented all necessary cultural and ethical measures to safeguard the privacy and confidentiality of respondents throughout the interview process and into perpetuity. The survey instrument was designed to collect only the essential data required for the study’s objectives. While GPS locations of interviews were recorded, this was done after obtaining informed consent and no additional personal information was gathered. After securely transferring all data from the LAs’ smartphones to MPCP's database, all data on the smartphone were deleted. MPCP restricted access to the dataset and provided me with an anonymized version containing only the data necessary to complete this analysis, containing no specific identifiers, such as GPS coordinates.

Analysis

Statistical Significance: We applied Bonferroni correction to account for multiple comparisons, defining a p-value between 0.05 and 0.01 as suggestive and $p < 0.01$ as significant [47-49].

Hypothesis Set 1 (H1): Our first set of hypotheses, *Species-Specific Perceptions* and *Generalized Perceptions,* examine whether respondents hold species-specific or generalized perceptions across the six species. To quantify overall perceptions, we calculated each respondent's six species-specific attitude scores (SSAS) by combining their responses to each species' four cost and four benefit statements. Benefit responses were assigned positive values ranging from +5 (strongly agree) to +1 (strongly disagree), while cost responses were assigned corresponding negative values from -5 (strongly agree) to -1 (strongly disagree). The scores sum for each species ranged from -16 (greatest perceived costs; -20 for ‘strongly agreeing’ with four cost statements, +4 for ‘strongly disagreeing’ with four benefit statements) to +16 (greater perceived benefits; +20 for ‘strongly agreeing’ with four benefit statements, -4 for ‘strongly disagreeing’ with four cost statements). This approach assumes that the ranked values for each cost or benefit statement are equivalent, permitting both within-subject and between-subject comparisons. Although this assumption lacks direct empirical evidence, similar methods suggest these scores may predict respondents' attitudes and behaviors [9].

We used Wilcoxon signed-rank tests to evaluate whether SSASs for each species differed significantly from those of other species. Significant differences in SSASs between a species and all others indicate support for *Species-Specific Perceptions*. In contrast, support for *Generalized Perceptions* is indicated by a lack of significant differences in SSASs between two or more species. We also present the percentages of respondents for each Likert-scale response to each benefit and cost statement for all species.

Hypothesis Set 2 (H2): Our second set of hypotheses, *ID Does Not Correlate with Perceptions* and *ID Correlates with Perceptions*, examines whether respondents' ability to identify a species correctly correlates with their perceptions. We quantified species identification ability by counting the number of correctly identified photos of each species (0-3). We used within-subject, two-sample Wilcoxon signed-rank tests to assess differences in identification rates across species and specific photos (flank, head-on, lying down). Although we considered developing a weighted scoring system to assess identification ability, such as accounting for the difficulty of identifying each photo (e.g., different postures) or the visual similarity between species, we lacked prior data to determine appropriate weights. Consequently, we opted for a binary classification: respondents who correctly identified all three photos of a species were classified as able to correctly identify it, while those who misidentified one or more photos were classified as likely to misidentify it. While this binary approach is more straightforward than a weighted system, using three photos per species provides a more comprehensive and robust assessment of identification ability than previous studies, which often relied on a single photo per species. However, we acknowledge the limitations of this method (see Discussion).

To evaluate H2, we employed Wilcoxon rank-sum tests to compare SSASs between respondents who correctly identified a species and those who did not. A lack of significant differences indicates support for *ID Does Not Correlate with Perceptions*, while significant differences indicate support for *ID Correlates with Perceptions*. For any species where *ID Correlates with Perceptions* are supported, we proceed to test our third set of hypotheses (H3).

Hypothesis Set 3 (H3): Our third set of hypotheses, *Misapplied* and *Diverging Perceptions*, evaluates whether individuals' ability to identify a species (A) influenced their perceptions due to confusion with another species (B). To evaluate H3, we identified respondents who misidentified species A as B and then used Wilcoxon rank-sum tests to compare differences in SSASs for species A and B between respondents who confused the two and respondents who correctly identified both species. To ensure robustness, we refined our criteria for the two groups of respondents: only respondents who misidentified species A exclusively as B and correctly identified all photos of B were included in the misidentification group, and only those who correctly identified all photos of both species were included in the correct identification group. A minimum of six respondents was required for comparisons to enhance statistical power. In cases where more than six respondents misidentified photos of species A as another species (C), an additional H3 test was conducted between those two species. Support for

Misapplied Perceptions is indicated by a significantly smaller difference in SSASs between species A and B by respondents who misidentified species A as B, compared to the difference in perceptions between the two species by respondents who correctly identified both. In comparison, a significantly greater difference in perceptions between the two species among respondents who misidentified A with B and respondents who correctly identified both species indicates support for *Diverging Perceptions*.

Regardless of which hypothesis was supported, we used Wilcoxon signed-rank tests to explore further how respondents within each group (i.e., respondents who confused species A with B and correctly identified B, and respondents who correctly identified both species) perceived both species. This approach allows for nuanced interpretations of the mechanisms influencing perceptions.

Socioeconomic Correlates: We also explored potential correlations of other socioeconomic factors on SSASs and species identification ability and discussed our results in Appendix 1 – Socioeconomic Correlates. For categorical attributes (e.g., zones, land lease to a conservancy, religion, occupation), we used Wilcoxon rank-sum tests to compare SSASs and the number of correctly identified photos for each species between respondent groups. For continuous attributes (e.g., age, education level), we assigned numeric values and used Kendall's rank correlation tests to assess correlations with SSASs and the number of correctly identified photos for each species.

Results

The Mara Predator Conservation Programme (MPCP) Lion Ambassadors (LAs) completed 300 interviews between November 22nd, 2021, and January 6th, 2022. Due to entry errors, 17 interviews conducted by one LA were discarded, leaving 283 interviews for analysis. This represents a 94.3% response rate.

Species-Specific vs. Generalized Perceptions (H1)

All respondents answered all eight statements about each carnivore species, except for leopards, which had 282 responses due to an error in one interview. The highest median species-specific attitude scores (SSASs) were for cheetahs, followed by leopards, African wild dogs (AWDs), lions, striped hyenas, and spotted hyenas (Table 3-1).

We found significant differences in individual SSASs between pairs of species for nearly all species-pairs (two-sample Wilcoxon signed-rank tests), except AWDs and lions (Table 3-1, Appendix 2: Comparisons between SSASs within respondents – Table 3-A2-1). Although this comparison did not reach the statistical threshold for suggestive differences, the effect size is large. These results largely support *Species-Specific Perceptions*, indicating that most respondents held unique perceptions about each carnivore species.

Table 3-1: Comparison of Species-Specific Attitude Scores (SSASs) across each species using within-subject, two-sample Wilcoxon signed-rank tests

Species	**Mean SSAS**	**Median SSAS** (Q1 to Q3)	**V-value** (vs. next species down)	**p-value** (vs. next species down)
Cheetah (n = 283)	+ 1.16	+1 (-2 to +4)	15338	0.003**
Leopard (n = 282)	+ 0.5	0 (-2 to +3)	15378	0.03*
African Wild Dog (n = 283)	+ 0.03	0 (-3 to +3)	14244	0.06
Lion (n = 283)	- 0.34	0 (-3 to +2)	20182	<0.001**
Striped Hyena (n = 283)	-1.29	-2 (-5 to +2)	8294	<0.001**
Spotted Hyena (n = 283)	-2.96	-3 (-6 to 0)	-	-

We report the results of the Wilcoxon signed-rank tests comparing SSASs between each species and the species with the next lowest median SSAS.
Pairwise comparisons across all species appear in Appendix 2: Comparison between SSASs Within Respondents – Table 3-A2-1.
** Bonferroni corrections signifying a significant behavior change, $p \leq 0.01$.
* Bonferroni corrections signifying a suggestive behavior change, $0.05 \geq p > 0.01$.

The greatest number of respondents 'strongly agreed' that seeing cheetahs is enjoyable, that they play an important ecological role, are important for their employment/income, and are essential for tourism (Figure 3-4). The greatest number also 'strongly agreed' that cheetahs pose risks to their own and other people’s livestock and to themselves or their families, while the greatest number 'agreed' (rather than 'strongly agreed') that cheetahs pose risks to other members of the community (Figure 3-5).

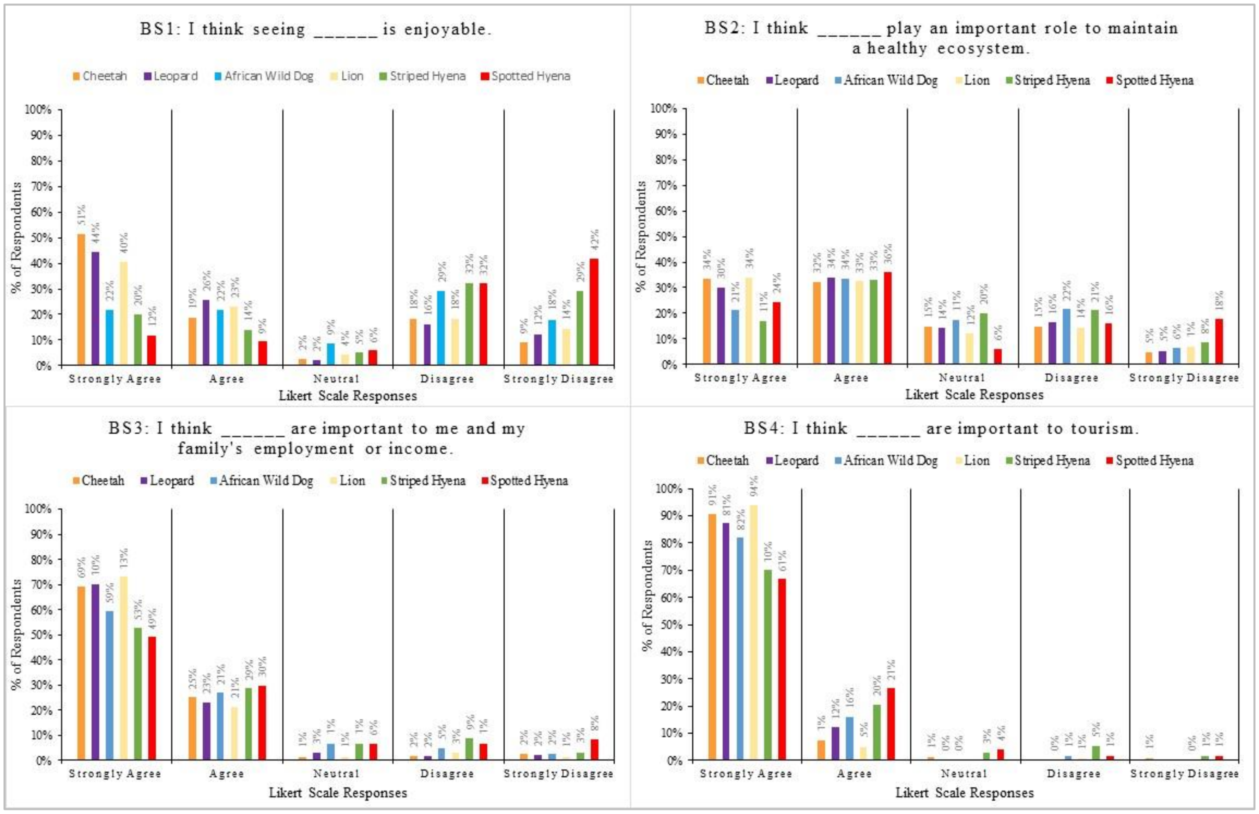


Figure 3-4: Distribution of responses to benefit statement 1 (BS1; top left), BS2 (top right), BS3 (bottom left), and BS4 (bottom right) as a percentage of respondents.

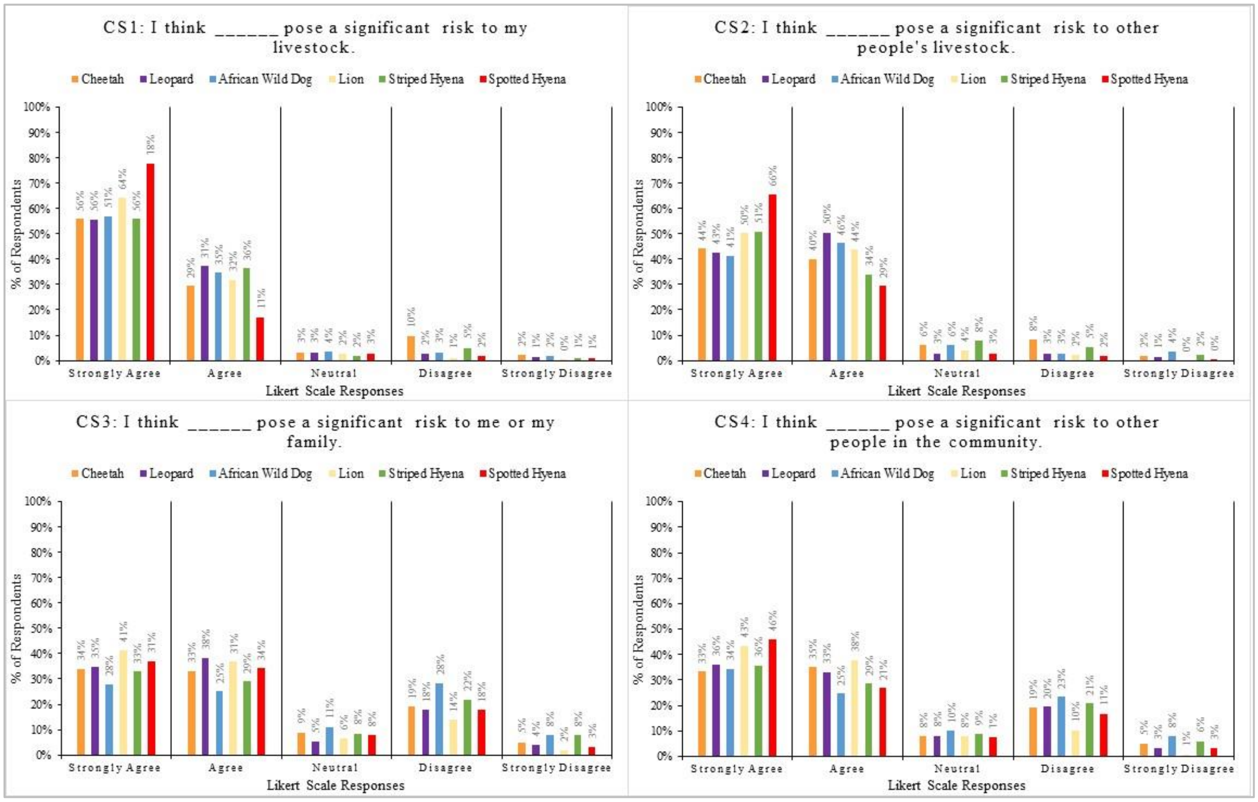


Figure 3-5: Distribution of responses to cost statement 1 (CS1; top left), CS2 (top right), CS3 (bottom left), and CS4 (bottom right) as a percentage of respondents.

The greatest number of respondents 'strongly agreed' that seeing leopards is enjoyable, that they play an important ecological role, and that they are important for their employment/income, while the greatest number 'agreed' that they are important for tourism (Figure 3-4). The greatest number also 'strongly agreed' that leopards pose risks to their own and other people’s livestock and to other community members, while the greatest number 'agreed' that they pose risks to themselves or their families (Figure 3-5).

The greatest number of respondents 'strongly agreed' that AWDs are important for their employment/income and that they play an important ecological role, 'agreed' that they are important for tourism, and 'disagreed' that seeing them is enjoyable (Figure 3-4). The greatest number also 'strongly agreed' that AWDs pose risks to their livestock and to other people in the community, while the greatest number 'agreed' they pose risks to other people’s livestock. Responses were nearly evenly split between 'strongly agree' and 'disagree' regarding whether AWDs pose risks to the respondents themselves or their families (Figure 3-5).

The greatest number of respondents 'strongly agreed' that seeing lions is enjoyable, that they play an important ecological role, are important for their employment/income, and are important for tourism (Figure 3-4). The greatest number also ‘strongly agreed’ that lions pose risks to their own and other people’s livestock and themselves, their families, and other people in the community (Figure 3-5).

The greatest number of respondents 'strongly agreed' that striped hyenas are important for their employment/income and play an important ecological role, 'agreed' that they are important for tourism, and 'disagreed' that seeing them is enjoyable (Figure 3-4). Additionally, the greatest number 'strongly agreed' that striped hyenas pose risks to their own and other people’s livestock and to themselves, their families, and others in the community (Figure 3-5).

The greatest number of respondents 'strongly agreed' that spotted hyenas are important for their employment/income and that they play an important ecological role, 'agreed' that they are important for tourism, and 'strongly disagreed' that seeing them is enjoyable (Figure 3-4). The greatest number also 'strongly agreed' that spotted hyenas pose risks to their own and other people’s livestock and to themselves, their families, and other people in the community (Figure 3-5).

<u>ID Does Not Correlate with Perceptions vs. ID Correlates with Perceptions (H2):</u>

All 283 respondents were shown three photos of each of the six focal species, except for leopards and striped hyenas, which had 282 responses due to errors in two interviews (Table 3-2). The greatest number of respondents correctly identified all three photos of lions (98%), followed by cheetahs (84%), spotted hyenas (82%), leopards (78%), and AWDs (62%). The exception was a majority of respondents misidentified one or more photos of striped hyenas (40% correctly identified all three photos). Within-subjects tests found significant differences in individual ability to identify each species except between cheetahs and spotted hyenas (Table 3-2; Appendix 3: Comparison of Species Identification Ability Within Respondents – Table 3-A3-1).

Table 3-2: Comparisons of individual ability to identify all three photos of each species using within-subject, two-sample Wilcoxon signed-rank tests

Species	Correct Identification (n of Respondents)	Misidentification (n of Respondents)	# of Photos Identified Median (Q1 to Q3)	V-value (vs. next species)	p-value (vs. next species)
Lion (n = 283)	276	7	3 (3 to 3)	1097	<0.001**
Cheetah (n = 283)	239	44	3 (3 to 3)	1101	0.63
Spotted Hyena (n = 283)	233	50	3 (3 to 3)	2238	0.001**
Leopard (n = 282)	219	63	3 (3 to 3)	5719	<0.001**
AWD (n = 283)	175	108	3 (2 to 3)	9094	<0.001**
Striped Hyena (n = 282)	113	169	2 (1 to 3)	-	-

We report the results of Wilcoxon signed-rank tests comparing respondents' abilities to correctly identify all three photos of each species with those of the species having the next highest percentage of respondents correctly identifying all three photos.
Pairwise comparisons across all species appear in Appendix 3: Species Identification – Table 3-A3-1.
Correct Identification required respondents to identify all three photos of that species correctly.
Misidentification required respondents to misidentify ≥1 photo of that species.
AWD refers to African wild dogs.
** Bonferroni corrections signifying a significant behavior change, $p \leq 0.01$.
* Bonferroni corrections signifying a suggestive behavior change, $0.05 \geq p > 0.01$.

For lions, the lying-down photo was misidentified most frequently, while the head-on and flank photos were misidentified at the same rate (Table 3-3). However, respondents' identification ability did not differ statistically across lion photos (Appendix 3: Comparison of Species Identification Ability Within Respondents – Table 3-A3-2).

For cheetahs, the head-on photo was most frequently misidentified, followed by the lying-down, then flank photo (Table 3-3). Results indicate that respondents identified the flank more often than the head-on photo (V = 326, p = 0.03), but there was no statistical difference between other pairwise comparisons (Appendix 3: Table 3-A3-2).

For spotted hyenas, the lying-down photo was most frequently misidentified, followed by the head-on, then flank photo (Table 3-3). Individuals were more likely to correctly identify both flank and head-on photos than the lying-down photos (vs. flank: $V = 677$, $p < 0.001$; vs. head-on: $V = 704$, $p = 0.001$), but there was no difference between the flank and head-on photos (Appendix 3: Species Identification – Table 3-A3-2).

For leopards, the head-on photo was misidentified most frequently, followed by the lying-down, then flank photo (Table 3-3). However, respondents' identification ability did not differ statistically across leopard photos (Appendix 3: Species Identification – Table 3-A3-2).

For AWDs, the head-on photo was most frequently misidentified, followed by the lying-down, then flank photo (Table 3-3). Individuals were more likely to correctly identify the flank photo than either the head-on ($V = 1556$, $p < 0.001$) or lying-down photos ($V = 833$, $p < 0.001$), but there was no difference between the head-on and lying-down photos (Appendix 3: Species Identification – Table 3-A3-2).

For striped hyenas, the lying-down photo was misidentified most frequently, followed by the head-on, then flank photo (Table 3-3). Individuals were more likely to correctly identify the flank photo than either the head-on ($V = 4233$, $p < 0.001$) or lying-down photos ($V = 1024$, $p < 0.001$) and were also more likely to correctly identify the head-on than the lying-down photo ($V = 1376$, $p = 0.004$).

Table 3-3: Number of respondents who misidentified each photo of all six species.

Species/Photo	**Misidentified** (n of Respondents)		
	Flank	Head-on	Lying-down
Lion (n = 7)	2	2	6
Cheetah (n = 44)	14	26	17
Spotted Hyena (n = 50)	7	12	33
Leopard (n = 63)	26	37	30
AWD (n = 108)	36	78	66
Striped Hyena (n = 169)	72	95	137

n in parentheses next to each species name refers to the total number of respondents who misidentified ≥1 photo of that species.
AWD refers to African wild dogs.

H2 Test: We compared SSASs between respondents who correctly identified each species and those who misidentified them. For cheetahs, lions, and striped hyenas, there was no significant difference in SSASs between the two groups (cheetahs: W = 94005, p = 0.70; lions: W = 2787, p = 0.10; striped hyenas: W = 9507, p = 0.95; Figure 3-6), supporting *ID Does Not Correlate with Perceptions* for these species.

In contrast, respondents who correctly identified leopards and spotted hyenas had significantly higher (positive) SSASs than those who misidentified them (leopards: W = 10598, p < 0.001; spotted hyenas: W = 11127, p = 0.04; Figure 3-6). These findings support *ID Correlates with Perceptions* for these species. Additionally, while our test for AWDs did not meet the statistical threshold, respondents who correctly identified AWDs tended to have higher SSASs than those who misidentified them (W = 11172, p = 0.07; Figure 3-6). Given the significant support for *ID Correlates with Perceptions* for leopards and spotted hyenas and the marginal support for AWDs, these three species will be the focus of our tests between *Misapplied* and *Diverging Perceptions* (H3).

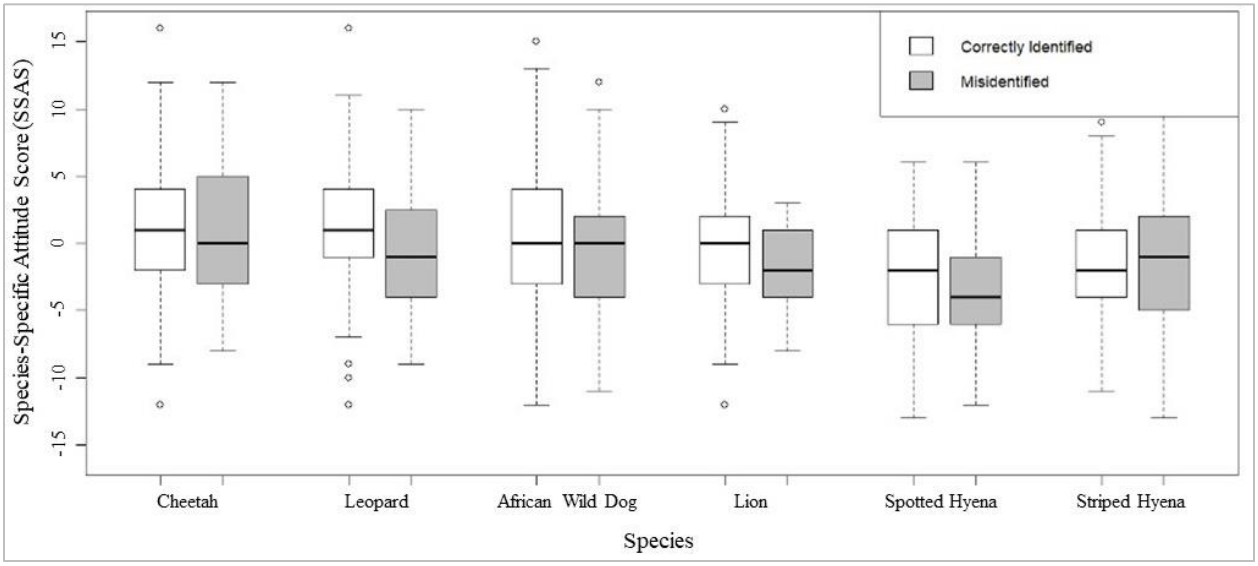


Figure 3-6: Grouped comparison of SSASs for cheetahs, leopards, lions, AWDs, spotted, and striped hyenas between respondents correctly identifying each species (white boxes) and those who misidentified them (gray boxes). Box plots depict the median (dark horizontal line), 1st & 3rd quartiles (boxes above and below the median), lower and upper quartiles (error bars), and outliers (open circles above the error bars).

Misapplied vs. Diverging Perceptions (H3)

Leopard: Of the 63 respondents who misidentified at least one leopard photo, 58 misidentified it as a cheetah, two as a lion, one as a spotted hyena, and one as a striped hyena. Therefore, we designate leopards as species A and cheetahs as species B. We compared the differences in SSASs between leopards and cheetahs for 36 respondents who misidentified leopard photos as cheetahs while correctly identifying all cheetah photos to 198 respondents who correctly identified all photos of both species.

We found no significant difference between our two sets of respondents when comparing the differences in SSASs for leopards and cheetahs (mean SSAS = -0.5 vs. mean SSAS = -0.49; W = 3761, p = 0.60; Figure 3-7). However, respondents who made this misidentification had significantly lower (more negative) SSASs for both leopards and cheetahs compared to those who correctly identified all photos of both species (leopard: W = 4883, p < 0.001; cheetah: W = 4593.5, p = 0.006; Figure 3-7). Additionally, respondents in both groups showed similar SSASs for the two species (Misidentified Leopard: V = 5222, p = 0.11; Correctly Identified Leopard: V = 124, p = 0.11; Figure 3-7). Therefore, while we found no evidence for either H3 hypothesis, we infer that misidentifying leopard photos as cheetahs is associated with more negative attitudes toward both species.

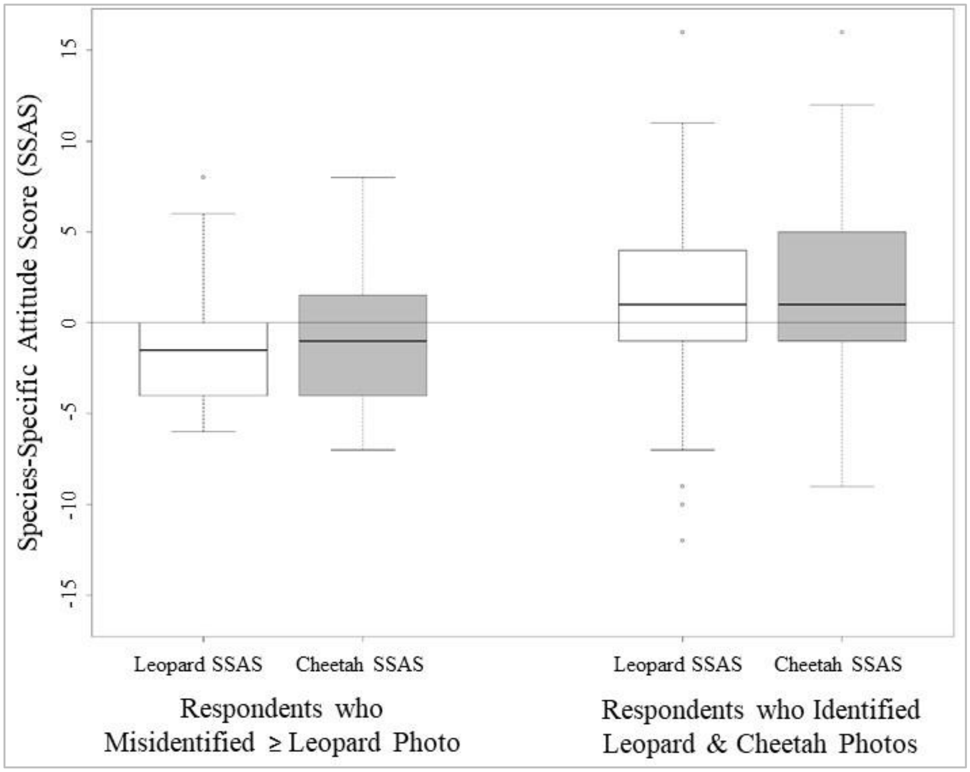


Figure 3-7: Grouped comparison of SSASs for leopards and cheetahs between respondents who misidentified at least one leopard photo as a cheetah (left side of the graph) and those who correctly identified all three photos of both species (right side of the graph). Box plots depict the median (dark horizontal line), 1st & 3rd quartiles (boxes above and below the median), lower and upper quartiles (error bars), and outliers (open circles above the error bars).

Spotted Hyena: Of the 50 respondents who misidentified at least one spotted hyena photo, 21 misidentified it as cheetah, six as AWD, six as striped hyena, five as lion, four as leopard, two as domestic dog, two as jackal, one as bat-eared fox, one as monkey, and one did not know. Therefore, we designate spotted hyenas as species A and cheetahs as species B. We compared the differences in SSASs between spotted hyenas and cheetahs for 15 respondents who misidentified spotted hyenas as cheetahs while correctly identifying all cheetah photos to 205 respondents who correctly identified all photos of both species.

We found no significant difference between our two sets of respondents when comparing the differences in SSASs for spotted hyenas and cheetahs and those who correctly identified both species (mean SSAS = -2.73 vs. mean SSAS = -4.28; W = 1325, p = 0.37; Figure 3-8). However, respondents who misidentified spotted hyenas as cheetahs had significantly higher (more positive) SSASs for spotted hyenas compared to those who correctly identified both species (W = 905.5, p = 0.008), while SSASs for cheetahs were similar between the two groups (W = 1198, p = 0.15; Figure 3-8). Additionally, both groups of respondents had significantly higher (more positive) SSASs for cheetahs than for spotted hyenas (Misidentified Spotted Hyena: V = 8.5, p = 0.01; Correctly Identified Spotted Hyena: V = 1306, p < 0.001; Figure 3-8). Therefore, while we found no evidence for either H3 hypothesis, we infer that misidentifying spotted hyenas as cheetahs was associated with more positive attitudes toward spotted hyenas without being associated with different attitudes toward cheetahs.

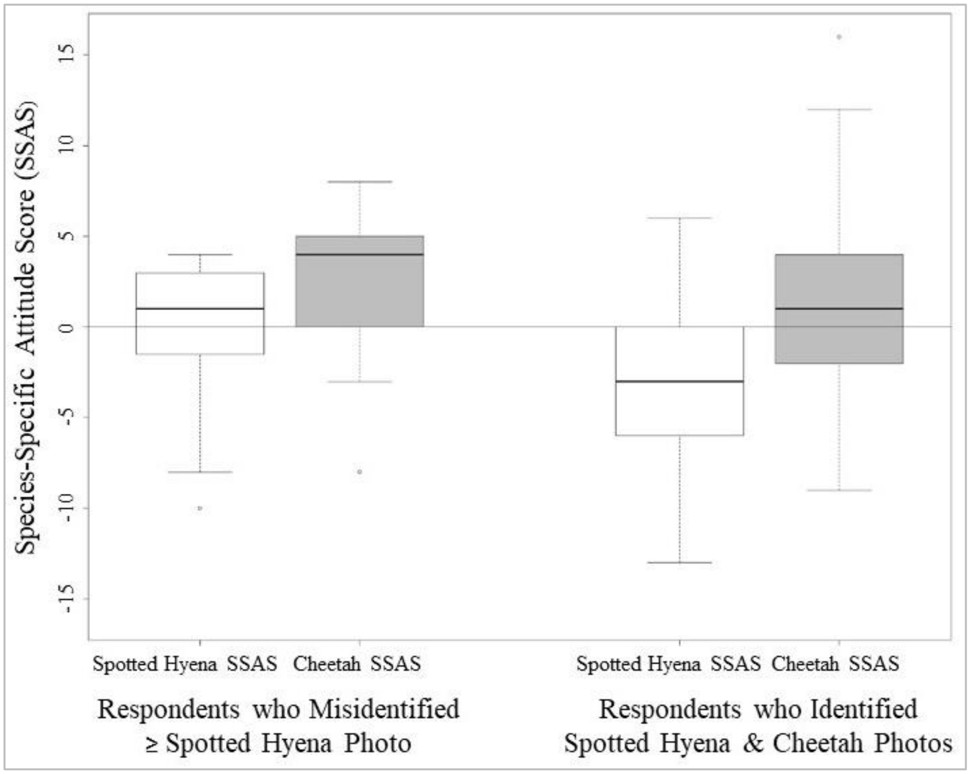


Figure 3-8: Grouped comparison of SSASs for spotted hyenas and cheetahs between respondents who misidentified at least one spotted hyena photo as a cheetah (left side of the graph) and those who correctly identified all three photos of both species (right side of the graph). Box plots depict the median (dark horizontal line), 1st & 3rd quartiles (boxes above and below the median), lower and upper quartiles (error bars), and outliers (open circles above the error bars).

African wild dog: Of the 108 respondents who misidentified at least one AWD photo, 32 misidentified it as spotted hyena, 18 as domestic dog, 12 as jackal, five did not know, three as cheetah, one as striped hyena, and one as bat-eared fox. Therefore, we designate AWDs as species A and spotted hyenas as species B. We then compared the differences in SSASs between AWDs and spotted hyenas for the 27 respondents who exclusively misidentified AWDs as spotted hyenas and correctly identified all spotted hyena photos and 153 respondents who correctly identified all photos of both species.

We found no significant difference between our two sets of respondents when comparing the differences in SSASs for AWDs and spotted hyenas and those who correctly identified both species (mean SSAS = 2.14 vs. mean SSAS = 3.45; W = 2265, p = 0.42; Figure 3-9). However, respondents who misidentified AWDs as spotted hyenas had significantly lower SSASs for AWDs compared to those who correctly identified both species (W = 2603, p = 0.03). Additionally, both groups had similar SSASs for spotted hyenas (W = 2359, p = 0.24; Figure 3-9), and both respondent groups had significantly higher SSASs for AWDs than for spotted hyenas (Misidentified AWD: V = 246, p = 0.03; Identified AWD: V = 7771, p < 0.001; Figure 3-9). Therefore, while we found no evidence for either H3 hypothesis, we infer that misidentifying AWDs as spotted hyenas was associated with lower perceptions towards AWDs without being associated with different attitudes toward spotted hyenas.

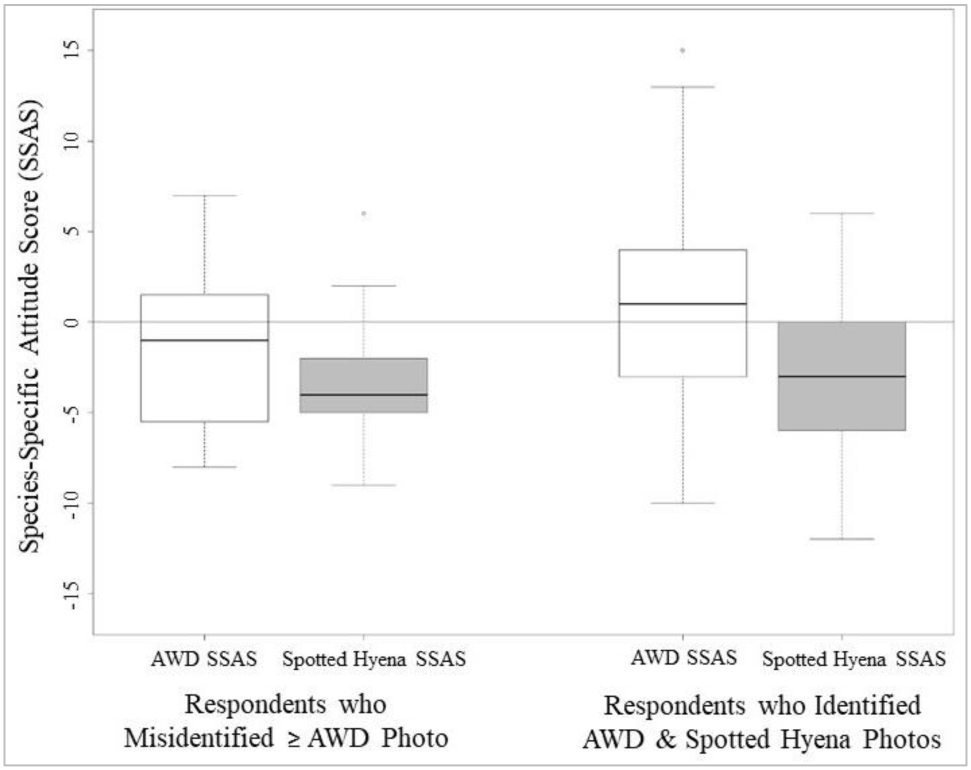


Figure 3-9: Grouped comparison of SSASs for African wild dogs (AWDs) and spotted hyenas between respondents who misidentified at least one AWD photo as a spotted hyena and those who correctly identified all three photos of both species. Box plots depict the median (dark horizontal line), 1st & 3rd quartiles (boxes above and below the median), lower and upper quartiles (error bars), and outliers (open circles above the error bars).

Discussion

We tested three sets of contrasting hypotheses to examine how individuals within a community living alongside multiple carnivore species perceive costs and benefits associated with each (H1) and how their ability to identify each species correctly correlates with their perceptions of it (H2 and H3). For H1, we found strong evidence supporting *Species-Specific Perceptions* for cheetahs, leopards, spotted hyenas, and striped hyenas, and weak evidence between lions and African wild dogs (AWDs), indicating that respondents held unique attitudes about each species. For H2, strong evidence found that *ID Correlates* *with Perceptions* for leopards and spotted hyenas, suggesting that respondents' ability to identify these species correctly was associated with their perceptions. There was also weak evidence that *ID Correlates with Perceptions* in the case of AWDs. In contrast, strong evidence found the *ID Does Not Correlate with Perceptions* for cheetahs, lions, and striped hyenas, indicating that identification ability was not associated with different perceptions about these species. For H3, we found no strong evidence supporting either *Misapplied* or *Diverging Perceptions* for leopards. However, weak evidence supported *Misapplied Perceptions* for spotted hyenas and AWDs, suggesting that respondents who confuse these species (species A) with another (species B) may have misapplied their perceptions of species B to species A.

Species-Specific & Generalized Perceptions (H1)

We found considerable variation among individual perceptions of the costs and benefits associated with all six carnivore species. This is consistent with prior research, though much of the previous work has focused primarily on the perceived risks different species pose to livestock [15, 32, 36, 37]. In contrast, our results offer important insights into how the differing costs and benefits associated with various species might lead to unique attitudes about each. This understanding is critical because these differences may predict varying attitudes and behaviors toward different species. For example, had our survey assessed only perceptions of livestock risk, we might have predicted that respondents hold the most negative attitudes toward spotted hyenas and lions, as the largest number of respondents 'strongly agreed' with all four cost statements for these species (Figure 3-5). However, while the fewest respondents 'strongly agreed' with three of the four benefit statements for spotted hyenas, the greatest number 'strongly agreed' with all four benefit statements for lions (Figure 3-6). As a result, our findings suggest that people likely hold more negative attitudes toward spotted hyenas than toward lions, which are associated with a variety of benefits, including providing income. Although studies differ on the importance of economic net benefits, several have associated personal income with more positive attitudes toward carnivores [23, 50-52]. Therefore, evaluating the unique patterns in perceptions across species can help identify the factors most likely to influence attitudes and behaviors toward each, guiding the development of targeted and effective conservation strategies.

Most respondents either 'strongly agreed' or 'agreed' that all six carnivore species posed a risk to their livestock (Figure 3-5). This broad agreement aligns with the concept of 'contagious conflict,' where individuals who perceive risk from one species are likely to perceive similar risk from others [6]. However, closer examination reveals notable differences in the level of risk attributed to each species. For example, 78% of respondents 'strongly agreed' that spotted hyenas posed a risk to livestock, followed by 64% for lions, and further declines for cheetahs (56%), leopards (56%), AWDs (57%), and striped hyenas (56%). Although a similar number of respondents 'strongly agreed' that the latter four species pose a risk to their livestock, responses among other respondents vary considerably, particularly for cheetahs. For example, 29% of respondents 'agreed' (rather than 'strongly agreed') that cheetahs posed a risk, compared to 37% for leopards, 35% for AWDs, and 36% for striped hyenas. Additionally, 10% 'disagreed' that cheetahs posed a risk, a notably higher rate of disagreement than for leopards (2%), AWDs (3%), or striped hyenas (5%). This variation suggests that respondents can differentiate levels of risk across species, even though some may generalize risk perceptions to multiple carnivores. Such generalizations might reflect actual risk similarities [53], species similarities, or broader contextual factors. For example, most respondents 'strongly agreed' that striped hyenas pose a risk to livestock despite their rarity in the Maasai Mara and limited role in livestock predation. This perceived risk could stem from a lack of direct experience with striped hyenas not posing a threat, leading individuals to rely on assumptions or perceived similarities with more familiar species known to cause livestock losses. Alternatively, respondents might attribute similar levels of risk to species with comparable physical traits (e.g., size, morphology), even when they recognize them as distinct species. Regardless of the causes of these generalizations, the variation in perceived risk among respondents underscores the importance of measuring species-specific perceptions better to predict individual attitudes and behaviors toward different species.

Another notable pattern we observed was that more respondents 'strongly agreed' with all four benefit statements for the three cat species – cheetahs, lions, and leopards – compared to AWDs and both hyena species. For example, 51% of respondents 'strongly agreed' that seeing cheetahs is enjoyable, followed by 44% for leopards and 40% for lions (Figure 3-4). In contrast, only 22% 'strongly agreed' that seeing AWDs is enjoyable, 20% for striped hyenas, and just 12% for spotted hyenas (Figure 3-4). This pattern aligns with previous research indicating that large cats tend to elicit more positive perceptions than other carnivores [54]. Perceiving greater benefits from cats may predict more positive attitudes and willingness to coexist with them. However, considerable variation in perceived benefits remains evident among the three cat species and between AWDs and hyenas. This underscores the importance of identifying the specific factors shaping perceptions of costs and benefits for each species rather than relying on undifferentiated assessments of carnivores as an assemblage. Next, we examine whether the ability to identify each carnivore species was associated with varying perceptions about them.

ID Does Not Correlate with & ID Correlates with Perceptions (H2)

Species Identification: Most respondents correctly identified all three photos of lions, cheetahs, spotted hyenas, leopards, and AWDs, whereas a minority correctly identified all three striped hyenas (Tables 3-2 & 3-4). These results provide valuable insights into respondents' identification abilities, particularly compared to prior studies conducted in the Maasai Mara that assessed identification for five of the six species (excluding striped hyenas) [23, 55]. Our study reported lower identification rates for all five species than the previous study (Table 3-4). While minor differences in these rates, such as those for lions, may reflect normal survey error margins, more significant discrepancies, such as those observed for AWDs, likely result from methodological differences. The earlier studies classified respondents as able to identify a species if they correctly identified a single flank photo. In contrast, our study required respondents to correctly identify three photos of each species, with individuals (carnivores) depicted in different body postures. When considering only the flank photos, our identification rates closely matched those reported in the earlier study (Table 3-4), and flank photos were the most frequently correctly identified for all six species (Table 3-3). This suggests that including head-on and lying-down photos contributed to our study's lower overall identification rates. Because carnivores are not always observed from the side in the wild, we believe our approach more accurately assesses respondents’ proficiency in correctly identifying each species under real-world conditions.

Table 3-4: Comparison of the percentage of respondents correctly identifying photos of lions, cheetahs, spotted hyenas, leopards, and African wild dogs (AWDs) between this study and Madsen and Broekhuis 2020.

	Correct Identification Rate		
Species	**Schuh et al. (2024)**		**Madsen and Broekhuis (2020)**
	ID 3 Photos	ID Flank Photo	ID Flank Photo
Lion	98%	99%	100%
Cheetah	84%	95%	90%
Spotted Hyena	82%	98%	99%
Leopard	77%	92%	84%
AWD	62%	87%	92%

Our results provide valuable context for understanding how identification abilities vary across human communities. For example, our findings align with other assessments of lion identification, where lions are almost universally correctly identified [6, 15, 32]. This consistency likely stems from lions' widespread presence in many parts of Africa [15, 32], their distinctive physical characteristics, such as their large size and lack of spots, and their prominence in social knowledge, media, and cultural narratives. These factors likely enhance recognition across communities. In contrast, our findings for the other five species diverge from similar surveys [6, 15, 32], indicating that most species' identification abilities can vary within and between communities. For example, one study reported that only 34% of respondents correctly identified cheetahs, a figure 50% lower than in our study [32]. This difference could stem from methodological variations, as the prior study used only a single flank photo. However, cheetahs were less common in that study area than in the Maasai Mara, which may also support the idea that species prevalence influences identification ability [15, 32]. Similarly, our study's low identification rate for striped hyenas likely reflects their relative rarity in the Maasai Mara. Additional factors, such as the cultural significance of particular species or unique socioeconomic variables within human communities, may also shape identification abilities (discussed in Appendix 2: Socioeconomic Correlates). These findings highlight the variability in identification abilities among individuals and communities, suggesting that if identification influences perceptions, it could play a critical role in shaping attitudes and behaviors toward different species.

H2 Test: Our results provide evidence that *ID Correlates with Perceptions* and *ID Does Not Correlate with Perceptions*, depending on the species. We found no evidence that the ability to identify cheetahs, lions, or striped hyenas was associated with different perceptions. However, identification ability was linked to differing perceptions of leopards, spotted hyenas, and AWDs. The reasons identification ability correlates with perceptions for some species but not others remain unclear. One explanation could relate to knowledge of species names and limitations in our survey methodology. Lion Ambassadors (LAs) gave respondents a photo of each species and mentioned its name while articulating the cost and benefit statements during the survey. As a result, respondents may have answered based on their familiarity with the species name or their recognition of the photo. If a species name is widely recognized in the community, even by those unable to identify its photo, our methodology may not fully isolate the effect of identification ability on perceptions. This explanation seems plausible for the three species supporting *ID Does Not Correlate with Perceptions*. Cheetahs and lions are common in the Maasai Mara and receive significant attention from tourism, media, and cultural narratives, making their names widely known. While most respondents misidentified striped hyenas, anecdotal evidence from MPCP employees suggests they were more prevalent in the past. Stories and cultural knowledge about striped hyenas may persist in the community, allowing respondents to recognize their name even without direct experience identifying them in the wild. To address this limitation, future surveys should avoid naming species aloud. Instead, respondents could be asked to answer cost and benefit statements based solely on displayed photos to better isolate the association of identification ability and perceptions.

Although some respondents likely answered each cost and benefit statement for leopards, spotted hyenas, and AWDs based on their familiarity with the species name, our finding that identification ability was associated with differing perceptions suggests the majority relied more on the photo displayed. For all three species, respondents who misidentified them had lower species-specific attitude scores (SSASs) than those who correctly identified them. These results challenge prior studies suggesting that identification ability primarily correlates with perceived risks to livestock [41]. Instead, they align with evidence indicating that individuals who misidentify species may hold more negative attitudes toward them [15]. This highlights how limited identification ability could contribute to negative perceptions, even when respondents recognize the species name but cannot accurately identify it visually.

One potential explanation for this result across all three species is that individuals less knowledgeable about certain species feel more anxious about the possible costs they could impose and are less aware of the benefits they may provide. For example, we found that pastoralists were more likely to misidentify leopards and held lower SSASs for them than respondents working in the tourism industry (Appendix 2: Socioeconomic Variables – Figures 3-A1-7 & 3-A1-8). This greater misidentification rate suggests pastoralists may be less knowledgeable about leopards, possibly due to the species' elusive and crepuscular nature in the Maasai Mara. Leopards often inhabit cryptic riparian ecosystems where livestock seldom graze, contrasting with more diurnal and less elusive carnivores like cheetahs and spotted hyenas, commonly active during the day in open landscapes where livestock are present. The lead author's (B.S.) personal experience locating leopards in the Maasai Mara supports this, as leopards are typically found in habitats that make direct encounters with pastoralists less likely. Without such encounters, pastoralists may have fewer opportunities to observe leopards killing livestock or see tourists watching leopards, reducing their direct experiences with the species. This lack of exposure may result in fewer perceived net benefits, explaining the lower SSASs. While we cannot rule out that a similar lack of knowledge among those who misidentified spotted hyenas and AWDs contributed to their lower SSASs, we found no socioeconomic variables that explain both a lack of knowledge and lower SSASs for these species.

Another potential explanation for why individuals who misidentified leopards, spotted hyenas, or AWDs had lower SSASs for each is that they may have confused these species with others [15, 41]. Previous studies have demonstrated that leopards and AWDs are frequently mistaken for other species [6, 15, 32, 41, 43]. This visual confusion may lead individuals to misapply their perceptions of one species onto another, suggesting that the perceptions reported by those who misidentified leopards, spotted hyenas, or AWDs might instead reflect their attitudes toward the species they confused them with. We explore this possibility further in our third set of hypotheses (H3).

Misapplied Perceptions vs. Non-Misapplied Perceptions (H3)

Leopards: Most respondents who misidentified one or more leopard photos confused them with cheetahs (92%). This is unsurprising given the visual similarities between the two species and aligns with previous studies reporting similar confusion [6, 15, 32, 41]. According to *Misapplied Perceptions*, respondents who confuse leopards (species A) with cheetahs (species B) would hold more similar perceptions about both species than those who correctly identify both. In contrast, *Diverging Perceptions* predicts that respondents who confuse leopards with cheetahs would exhibit greater differences in their perceptions about both species compared to those who correctly identify them. However, our results provided no evidence to support either hypothesis.

Despite finding no evidence for *Misapplied Perceptions*, respondents who misidentified leopards had lower SSASs for both leopards and cheetahs than those who correctly identified both species (Figure 3-7). One potential explanation is 'blame displacement’ [56], where respondents attribute negative experiences caused by one species to others. For example, respondents who confuse leopards with cheetahs may blame cheetahs for the costs that the leopards cause. Indirect evidence strongly supports the idea that leopards may cause more significant conflict, particularly through livestock predation. Numerous studies on species-specific perceptions consistently rank leopards as posing a higher risk to livestock than other carnivores. These perceptions are further validated by data on actual livestock losses, which frequently attribute greater predation rates to leopards than cheetahs [15, 18, 32, 35, 37]. Alternatively, because respondents correctly identified cheetahs, their perceptions of cheetahs may more accurately reflect the actual costs and benefits posed by cheetahs. In this case, they might attribute more significant costs caused by cheetahs to leopards. Although this seems less likely, one study near Tsavo

National Park documented cheetahs killing sheep and goats while recording no livestock predation by leopards despite the presence of both species [34]. A similar pattern could occur in areas where habitat conditions favor cheetahs over leopards, leading to higher livestock losses to cheetahs. In the Maasai Mara, extensive open plains used for daytime grazing are better suited for cheetahs than leopards, which prefer more cryptic riparian ecosystems. This habitat difference might explain why respondents who experience more frequent losses to cheetahs have fewer encounters with leopards, increasing the likelihood of confusing the two species. Therefore, localized habitat and predation patterns may contribute to misidentification and differences in SSASs between these species.

Another explanation for why respondents who confused leopards with cheetahs had lower SSASs for both species is that their misidentification may stem from preexisting negative perceptions of one or both species. For example, these respondents might harbor a stronger dislike for cheetahs than those who correctly identified both species, leading them to associate leopards with cheetahs out of bias against similar-looking species or due to a lack of knowledge. Their lower SSASs for cheetahs could reflect cheetahs imposing greater perceived costs (discussed above) or arise from unrelated factors. Importantly, attitudes toward carnivores are not solely shaped by direct experiences of their costs and benefits but are also influenced by cultural beliefs and social norms [5, 6, 40]. As a result, respondents who dislike cheetahs may project their negative perceptions onto leopards or other visually similar species, reinforcing their lower SSASs for both.

Blame displacement and preexisting negative perceptions provide plausible explanations for why respondents had lower SSASs for both leopards and cheetahs. However, the correlative nature of our data prevents us from determining which factor, if either, is driving the observed patterns. Additionally, other unexamined factors may better explain these results. Therefore, experimental tests of attitudes, such as the one conducted by Slagle et al. (2013), would help validate our methods and strengthen inferences about the causes of attitudes.

Spotted Hyena: The largest group of respondents who misidentified one or more spotted hyena photos confused them with cheetahs (n = 21 of 50), but more than half misidentified at least one photo as another species. This suggests less consistent confusion between spotted hyenas and cheetahs compared to leopards and cheetahs. Still, this confusion is surprising, given the differences in body morphologies and pelage between these species. To our knowledge, no other studies have reported similar findings. According to *Misapplied Perceptions*, respondents who confuse spotted hyenas (species A) with cheetahs (species B) would hold more similar perceptions about both species than those who correctly identify both. In contrast, *Diverging Perceptions* predicts that respondents who confuse spotted hyenas with cheetahs would exhibit greater differences in their perceptions about both species compared to those who correctly identify them.

Despite the lack of support for *Misapplied Perceptions*, respondents who confused spotted hyenas with cheetahs had more positive perceptions of spotted hyenas than those who correctly identified both species. Meanwhile, both groups reported similar and greater (more positive) SSASs for cheetahs (Figure 3-8). This suggests weak evidence that the more positive perceptions of cheetahs held by respondents who confused the two species may have influenced their perceptions of spotted hyenas. This contrasts with 'blame displacement,' observed among respondents who confused leopards with cheetahs, suggesting respondents who confused spotted hyenas as cheetahs may have artificially more positive perceptions about spotted hyenas due to a phenomenon we term, 'displacement of tolerance.' Namely, tolerance for spotted hyenas, or their willingness to coexist with them, may be boosted by positive attitudes toward cheetahs. Indirect evidence strongly supports the idea that cheetahs may be associated with more significant net benefits, particularly through less frequent livestock predation than spotted hyenas [15, 32, 35, 37]. However, given that our data are only correlative, these results may not be causally linked. Future research should focus on studying individuals who misidentify these species to understand better the dynamics of this confusion and its impact on perceptions. In-depth interviews or narrative-based approaches could explore how respondents perceive and differentiate between these species, providing additional insight into the factors influencing their attitudes.

Implications for the protection and management of spotted hyenas arise. For example, if those individual humans who confuse spotted hyenas with cheetahs hold more positive perceptions about spotted hyenas, this could conceal or underestimate the net benefits of spotted hyenas, potentially leading managers to neglect necessary actions to mitigate their impact on people and livestock. Therefore, additional research may be needed to assess the actual costs spotted hyenas impose and develop interventions that address these impacts while promoting greater benefits.

African Wild Dogs: The largest group of respondents who misidentified one or more AWD photos confused them with spotted hyenas (n = 32 of 108), but over two-thirds misidentified at least one photo as one of six other species, most notably domestic dogs (n = 18) and jackals (n = 12). Other studies corroborate this pattern, showing AWDs are often confused with these species, likely due to visual similarities [32]. Additionally, AWDs are uncommon in the Maasai Mara [43], suggesting many respondents may lack direct experience with them, further contributing to their confusion with more familiar species. The consistent confusion among these four species indicates that future studies should explore how identification ability and perceptions of all four species may collectively influence attitudes. This study focused on individuals who confused AWDs with spotted hyenas. *Misapplied Perceptions* predicts that respondents who confused AWDs (species A) with spotted hyenas (species B) would have more similar perceptions of both species than those who correctly identified both. In contrast, *Diverging Perceptions* predicts greater differences in perceptions.

Despite the lack of significant support for *Misapplied Perceptions*, respondents who confused AWDs with spotted hyenas had lower SSASs (more negative) about AWDs than those who correctly identified both species. Meanwhile, both groups had similar and more negative SSASs about spotted hyenas (Figure 3-9). This suggests that visual confusion lowers perceptions of AWDs without affecting how respondents view spotted hyenas. Although this result aligns with the concept of ‘blame displacement,’ the mechanism differs from that observed among respondents who confused leopards with cheetahs, where confusion led to more negative perceptions of both species. Here, the misidentification of AWDs as spotted hyenas appears to impact perceptions of AWDs alone. These findings suggest that respondents may unintentionally attribute the higher costs they associate with spotted hyenas to AWDs due to visual confusion. Indirect evidence offers mixed evidence about which species is likely associated with lower net benefits. One study found similar attitudes toward AWDs and spotted hyenas [15], while others reported greater livestock predation by AWDs [35] or by spotted hyenas [32], indicating both species can impose significant costs in different contexts. However, given AWDs' rarity in the Maasai Mara, they are unlikely to cause widespread conflict, whereas the more common spotted hyenas are a known source of conflict. The rarity of AWDs may also contribute to respondents' limited direct experience with them, increasing the likelihood of confusion with spotted hyenas. As a result, it is plausible that respondents' more negative perceptions of AWDs reflect conflicts caused by spotted hyenas.

These findings have important implications for conservation and management strategies promoting coexistence with AWDs. If respondents hold more negative perceptions of AWDs due to confusion with spotted hyenas, reported perceptions of AWD-related costs may inaccurately reflect conflicts caused by spotted hyenas. This misattribution could lead to unnecessary interventions targeting AWDs for conflicts they do not cause. Redirecting management efforts and funding to address conflicts caused by spotted hyenas could more effectively improve perceptions of AWDs. Additionally, educational programs that help people distinguish between AWDs and spotted hyenas may further enhance perceptions of AWDs by reducing the likelihood of misplaced blame for the impacts of spotted hyenas.

Survey Limitations

Perceptions: Our measurements of species-specific perceptions come with several limitations. First, although we found variations in respondents' SSASs, these scores may not directly predict positive or negative overall attitudes toward a species or a willingness to coexist. For example, we observed positive SSAS for three species and negative SSASs for the other three (Table 3-1). However, a survey conducted by MPCP in the same community reported that 58% of respondents wanted to coexist with all carnivores [23]. Methodological differences could explain this discrepancy, such as the lack of species-specific questions in the previous survey. However, it is also possible that respondents with negative

SSASs for particular species are still willing to coexist with them, and vice versa. This limitation suggests that our approach's value lies in comparing SSASs between species. For example, our methods clearly indicate that respondents associated cheetahs with greater net benefits than spotted hyenas, suggesting they are likely more willing to coexist with cheetahs.

A second limitation of our species-specific measures of perceptions is the non-continuous nature of the ranked scale. While the five-point Likert scale allowed respondents to express varying levels of agreement, it may not have captured the full range of their perceptions. For example, a seven-point scale could have revealed a greater resolution of individual differences. However, since most of our comparisons were conducted within-subject, the scale is unlikely to significantly influence our findings.

Species Identification: Using multiple photos to assess respondents' species identification abilities also revealed certain limitations. First, while it is reasonable to conclude that a respondent who fails to identify a photo of species A correctly may be more likely to struggle at identifying A consistently in the wild, how to interpret cases where a photo of species B is misidentified as A remains unclear. For example, a respondent may accurately identify all three cheetah photos but misidentify a leopard photo as a cheetah. In such cases, we can infer that the respondent will likely identify cheetahs accurately in the wild. Still, it is unclear whether their misidentification of a leopard as a cheetah should diminish our confidence in their cheetah identification ability. Second, while using photos of animals in different body postures enhances the assessment, including additional photos depicting animals in varied environmental conditions, such as open landscapes, dense bushes, or trees, might provide a more comprehensive evaluation. These variables warrant further investigation. Nevertheless, Given the associations we found between identification ability and species perceptions, we recommend that future researchers studying attitudes toward carnivores carefully account for identification ability in their methods. Doing so may refine the measurement of species-specific perceptions and improve predictions about attitudes and behaviors. Incorporating diverse and realistic scenarios for identification tasks could further strengthen the reliability of findings and advance our understanding of how identification ability shapes human-wildlife interactions.

Species Confusion: Previous studies have acknowledged the occurrence of species misidentifications but have not systematically explored species confusion beyond mentioning its possibility [6, 15, 32]. Our data suggest species confusion is not random error. Rather, it systematically correlates to attitudinal data measured by structured questionnaires. We suggest researchers should consider margins of error in their measures of attitudes that relate to species confusion. Those margins will be species-specific and specific to their respondents. The margins of error will further reduce the likelihood of significant tests of hypotheses about attitudes because species confusion makes tests of differences between respondents more prone to error.

Using three photos for each species improved our assessment of respondents' ability to identify species but left uncertainties about their likelihood of confusing one species for another. Our goal was to use multiple photos to identify respondents who might consistently confuse species A with species B in the wild. For example, we would have greater confidence in a respondent confusing leopards with cheetahs if they misidentified all three leopard photos as cheetahs compared to someone who misidentified only one. However, because few respondents misidentified all three photos of a species as another, we categorized anyone who misidentified one or more photos of species A as species B as more likely to confuse those species. Grouping respondents in this way likely overestimated the number of individuals we identified as prone to species confusion. This could have introduced uncertainty into our third hypothesis set (H3). Specifically, if respondents included in the group likely to confuse species are not truly prone to confusion, they would also be unlikely to misapply perceptions. This suggests our H3 results may be conservative, as misapplied perceptions may be more prevalent among those consistently confusing species. To address this limitation, we recommend future research increase sample sizes to capture more respondents who consistently misidentify multiple photos or develop new survey methodologies to assess species confusion more accurately. These approaches will be essential for understanding how species confusion influences perceptions and determining whether it should be factored into predictions about attitudes and behaviors toward different species.

Conclusion

Our results suggest that individuals hold species-specific perceptions about the costs and benefits associated with different carnivore species, supporting our *Species-Specific Perceptions* hypothesis. This finding expands on previous research, demonstrating this pattern when considering different species' risk to livestock. Additionally, our results indicated that misidentifying certain species, cheetahs, lions, and striped hyenas, was not associated with different perceptions about them, supporting *ID Does Not Correlate with Perceptions*. However, misidentifying other species, such as leopards, spotted hyenas, and African wild dogs (AWDs), was associated with more negative perceptions, supporting *ID Correlates with Perceptions*. These findings led us to examine our third hypothesis set, *Misapplied Perceptions* and *Diverging Perceptions*, for leopards, spotted hyenas, and AWDs. While we found no significant evidence supporting either hypothesis, the analysis of perceptions among respondents who confused these species as others yielded valuable insights. For example, respondents who confused leopards with cheetahs exhibited more negative perceptions toward both species. This could be attributed to blame displacement, where confusion between leopards and cheetahs resulted in more negative perceptions of both. Alternatively, this confusion could stem from preexisting negative perceptions of spotted cats, leading to misidentification out of apathy. In the case of respondents who misidentified spotted hyenas as cheetahs, we theorized that their confusion may have led to artificially higher attitudes toward spotted hyenas due to a phenomenon we term displacement of tolerance, where respondents misapply positive perceptions of cheetahs to spotted hyenas. Similarly, for those who misidentified AWDs as spotted hyenas, we hypothesized that their confusion may have resulted in artificially lower attitudes toward AWDs due to blame displacement, where respondents mistakenly attribute the costs associated with spotted hyenas to AWDs.

The management implications of these findings depend on whether respondents hold artificially positive or negative perceptions about the species they are confused about. Artificially positive perceptions may lead to management interventions overlooking the true costs imposed by the species, requiring further research to identify these costs and develop appropriate management strategies. On the other hand, artificially negative perceptions might prompt unnecessary interventions aimed at mitigating costs that the misidentified species does not cause. Therefore, educational programs aimed at helping individuals differentiate between species could be particularly beneficial. In summary, these findings demonstrate that species misidentification can influence perceptions, a factor previously only discussed in passing in earlier studies [6, 15, 32, 41]. These insights have important implications for wildlife management and conservation efforts, underscoring the need to understand better how species misidentification and confusion can shape people's perceptions of different species.

Appendix 1: Socioeconomic Correlates

Results

All respondents were male. The majority (80%) reported leasing land to a conservancy, and 82% identified their primary occupation as pastoralism, with 14% working in the tourism sector, 3% as agriculturalists or businessmen, and 1% other occupations. Most respondents (69%) reported being Christian, while 31% followed traditional beliefs. In terms of education, 65% had no formal education, whereas 16% reported their highest level of education as primary, 13% as secondary and 6% as tertiary. Nearly all respondents reported owning livestock, with 98% owning cattle and 95% owning sheep and goats. The average number of livestock per household was 81.08 cattle and 123.02 shoats.

Zones: Respondents from old zones (1–10) correctly identified photos of cheetahs, leopards, lions, AWDs, and spotted hyenas at similar rates to those from new zones (11–15), but correctly identified photos of striped hyenas at higher rates (Wilcoxon rank sum test, W = 10291, p < 0.001; Figure 3-A1-1). Respondents from old zones had similar SSAS scores for spotted hyenas but scored higher for cheetahs (W = 9662, p = 0.01), leopards (W = 10498, p < 0.001), lions (W = 10736, p < 0.001), AWDs (W = 10736, p = 0.01), and striped hyenas (W = 10846, p < 0.001; Figure 3-A1-2).

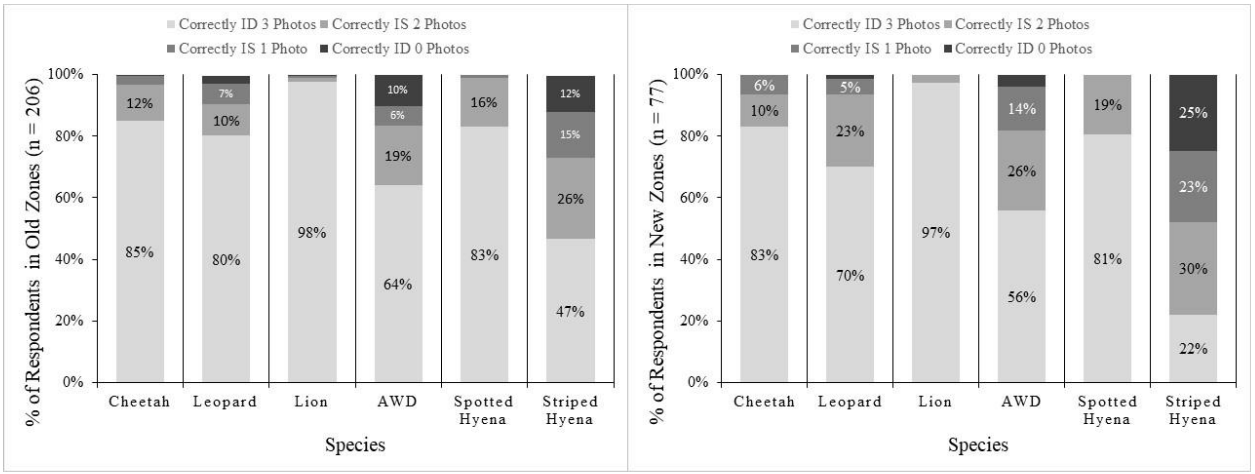


Figure 3-A1-1: The percentage of respondents from old zones, 1 – 10 (left graph), and new zones, 11 – 15 (right graph) that correctly identified 3 (lightest part of bars), 2, 1, and 0 (darkest part of bars) cheetah, leopard, lion, African wild dog (AWD), spotted hyena, and striped hyena photos. No data label was included if the percentage of respondents who correctly identified any number of photos was < 5%. Respondents from the old zones correctly identified more striped hyena photos.

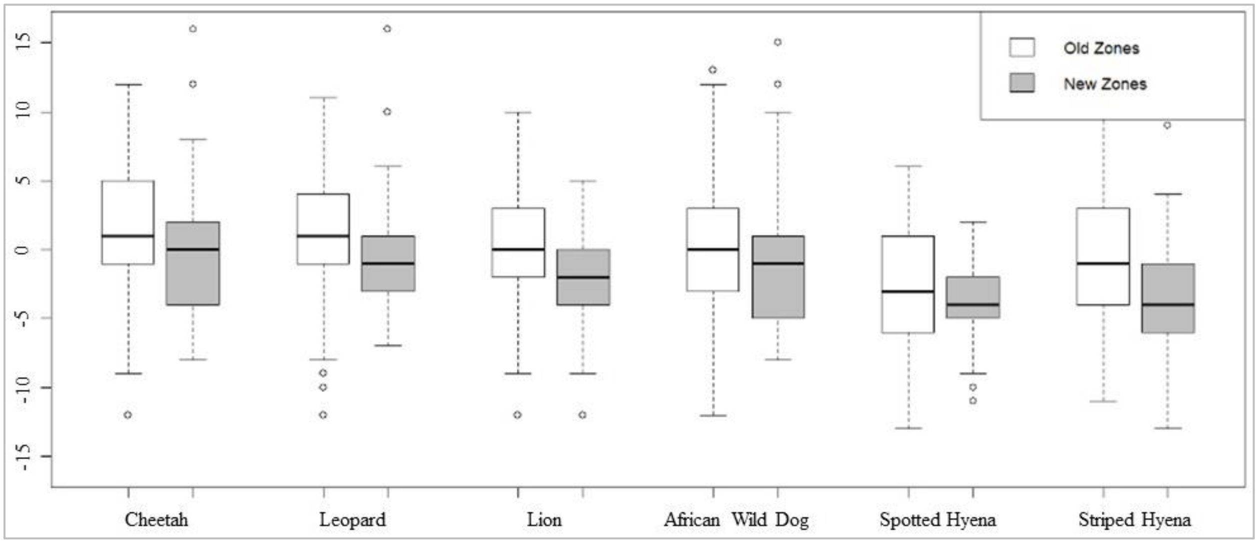


Figure 3-A1-2: Grouped comparison of SSAS for cheetahs, leopards, lions, AWDs, spotted, and striped hyenas between respondents from the old, 1 – 10 (white boxes), or new, 11 – 15, zones (grey boxes). Box plots depict the median (dark horizontal line), 1st & 3rd quartiles (boxes above and below the median), lower and upper quartiles (error bars), and outliers (open circles above the error bars). Respondents from the old zones scored a higher SSAS for cheetahs, leopards, lions, AWDs, and striped hyenas.

Conservancies: Respondents who lease land to a conservancy correctly identified photos of all six carnivore species at similar rates to those who did not (Figure 3-A1-3). However, respondents who lease land to a conservancy had higher SSASs for all six species than those who did not (cheetahs: W = 8087, p = 0.005; leopards: W = 8184, p = 0.003; lions: W = 8204, p = 0.002; AWDs: W = 8074, p = 0.005; spotted hyenas: W = 8744, p < 0.001; striped hyenas: W = 8080, p = 0.005; Figure 3-A1-4).

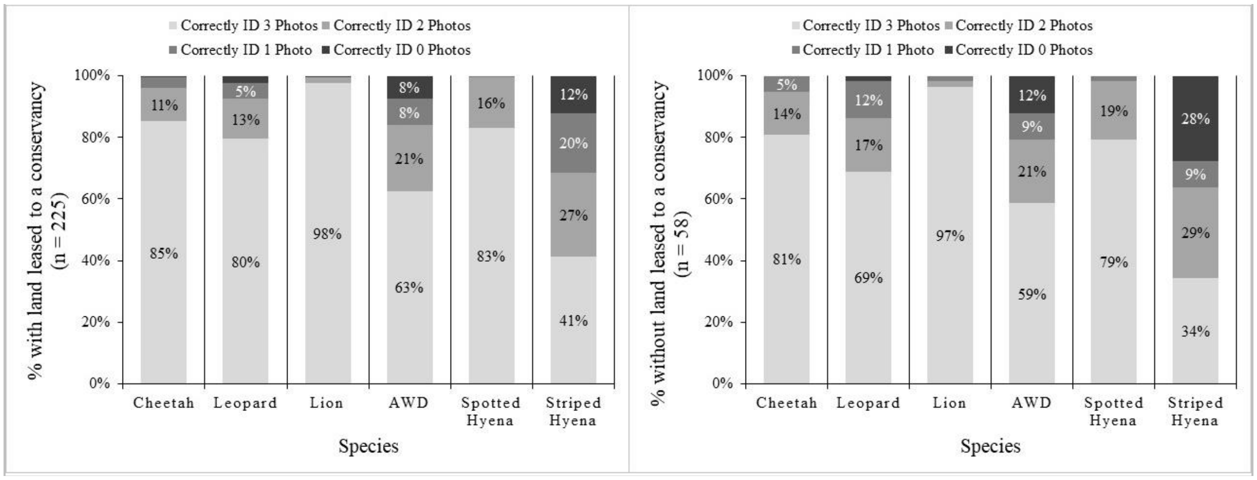


Figure 3-A1-3: The percentage of respondents who lease land to a conservancy (left graph) and non-owners (right graph) that correctly identified 3 (lightest part of bars), 2, 1, and 0 (darkest part of bars) cheetah, leopard, lion, African wild dogs (AWD), spotted hyena, and striped hyena photos. No data label was included if the percentage of respondents who correctly identified any number of photos was < 5%. Respondents in both groups correctly identified a similar number of photos for all six species.

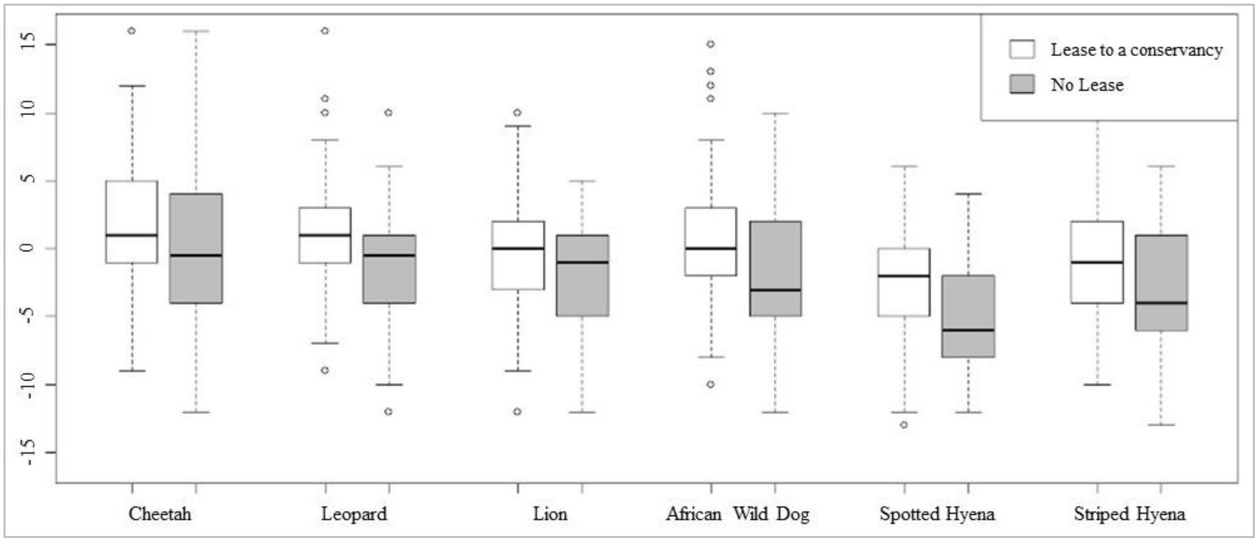


Figure 3-A1-4: Grouped comparison of SSAS for cheetahs, leopards, lions, AWDs, spotted, and striped hyenas between respondents who lease land to a conservancy (white boxes) and non-owners (grey boxes). Box plots depict the median (dark horizontal line), 1st & 3rd quartiles (boxes above and below the median), lower and upper quartiles (error bars), and outliers (open circles above the error bars). Respondents who lease land to conservancies scored a higher SSAS for all six species.

Religion: Christians and traditionalists correctly identified photos of all six carnivore species at similar rates (Figure 3-A1-5). Christians also had similar SSASs for cheetahs, leopards, lions, and spotted hyenas compared to traditionalists but had lower SSASs for AWDs (W = 7066, p = 0.02) and higher SSASs for striped hyenas (W = 9809, p = 0.04; Figure 3-A1-6).

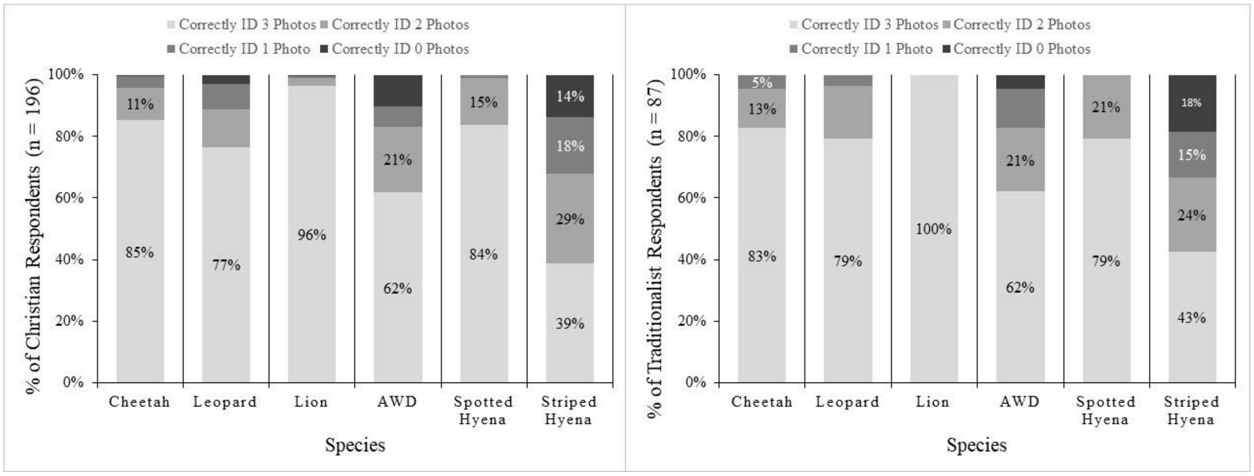


Figure 3-A1-5: The percentage of respondents who are Christian (left graph) and traditionalist (right graph) that correctly identified 3 (lightest gray part of bars), 2, 1, and 0 (darkest part of bars) cheetah, leopard, lion, African wild dog (AWD), spotted hyena, and striped hyena photos. No data label was included if the percentage of respondents who correctly identified any number of photos was < 5%. Respondents in both groups correctly identified a similar number of photos for all six species.

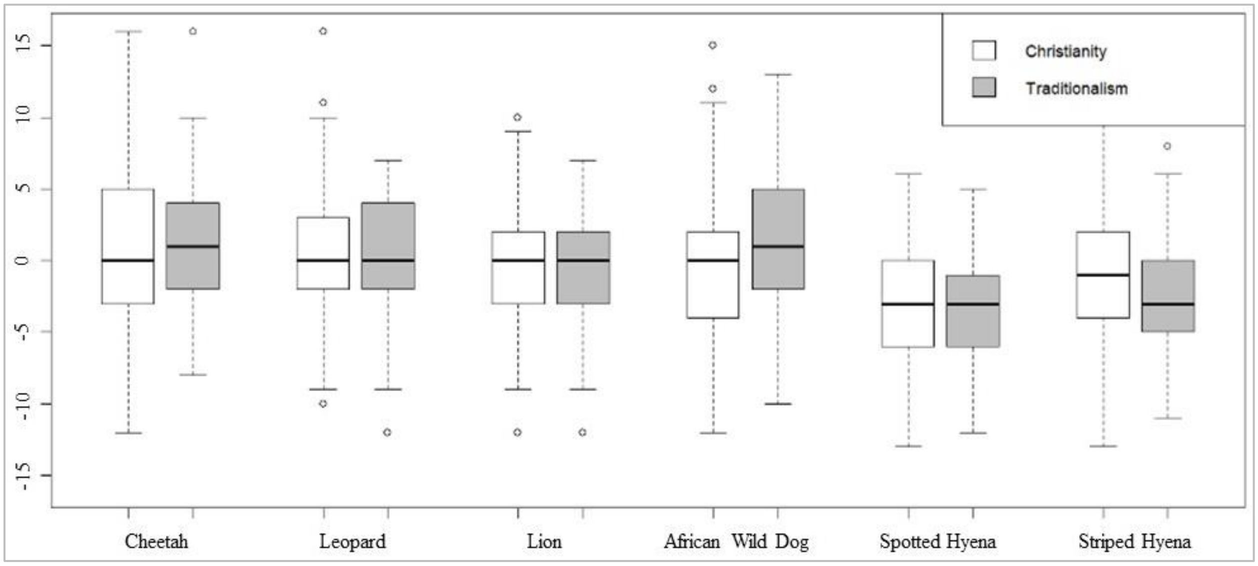


Figure 3-A1-6: Grouped comparison of SSAS for cheetahs, leopards, lions, AWDs, spotted, and striped hyenas between Christians (white boxes) and traditionalists (grey boxes). Box plots depict the median (dark horizontal line), 1st & 3rd quartiles (boxes above and below the median), lower and upper quartiles (error bars), and outliers (open circles above the error bars). Christians scored a lower SSAS for AWDs and a higher SSAS for striped hyenas.

Occupation: Respondents employed in the tourism industry correctly identified photos of cheetahs, lions, AWDs, spotted hyenas, and striped hyenas at similar rates to pastoralists but were better at identifying photos of leopards (W = 5501, p = 0.01; Figure 3-A1-7). Respondents employed in the tourism industry also had similar SSASs for cheetahs, lions, and striped hyenas compared to pastoralists but had higher SSASs for leopards (W = 5980, p = 0.003), AWDs (W = 5534, p = 0.05), and spotted hyenas (W = 5904, p = 0.006; Figure 3-A1-8).

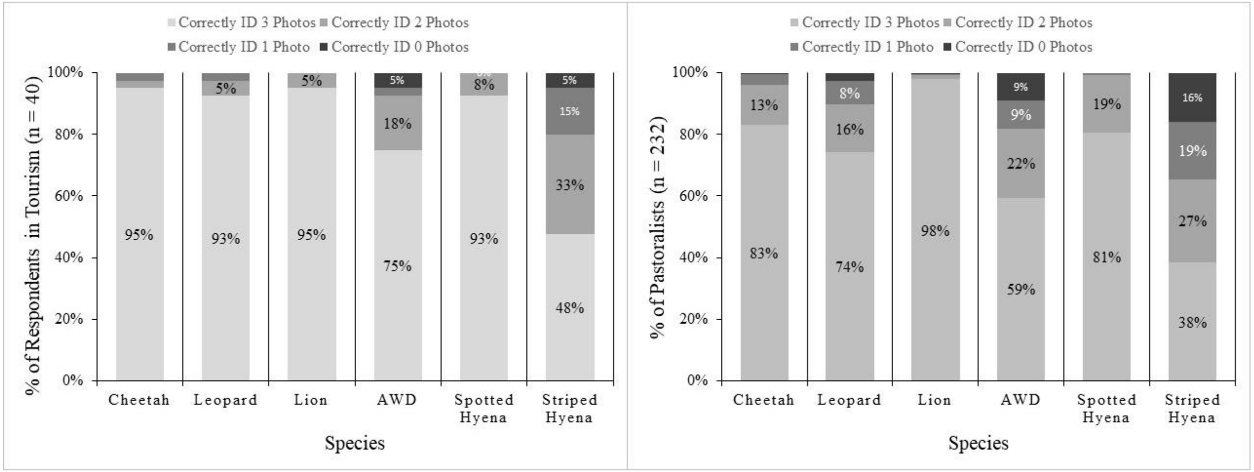


Figure 3-A1-7: The percentage of respondents in the tourism industry (left graph) and pastoralists (right graph) that correctly identified 3 (lightest part of bars), 2, 1, and 0 (darkest part of bars) cheetah, leopard, lion, African wild dog (AWD), spotted hyena, and striped hyena photos. No data label was included if the percentage of respondents who

correctly identified any number of photos was < 5%. Respondents in the tourism industry correctly identified more leopard and striped hyena photos.

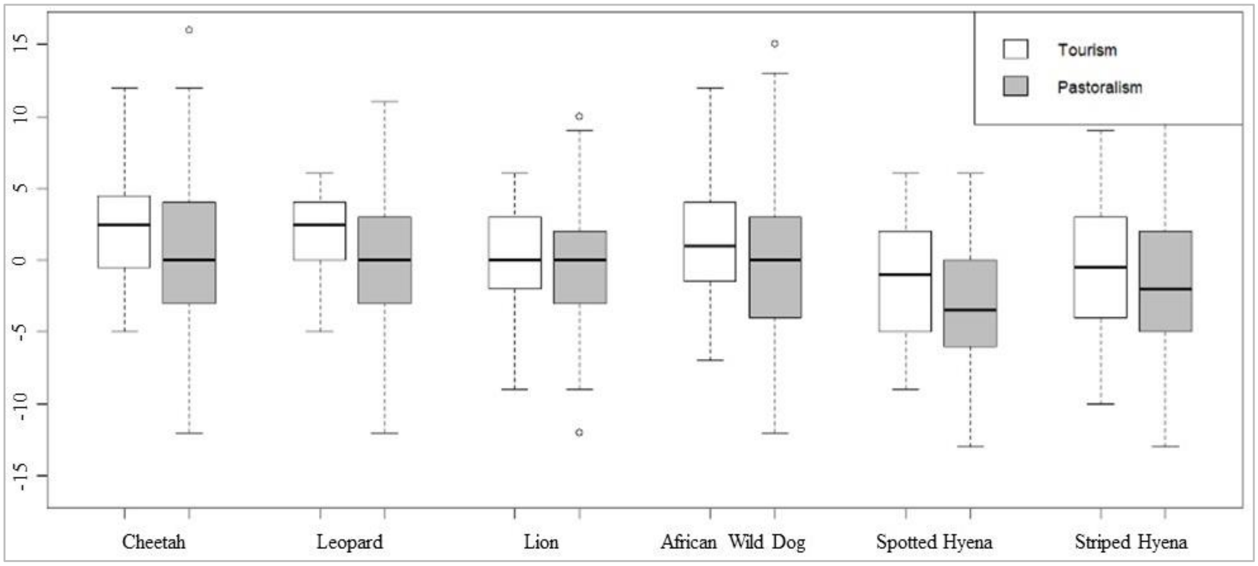


Figure 3-A1-8: Grouped comparison of SSAS for cheetahs, leopards, lions, AWDs, spotted, and striped hyenas between respondents employed in the tourism industry (white boxes) and pastoralists (grey boxes). Box plots depict the median (dark horizontal line), 1st & 3rd quartiles (boxes above and below the median), lower and upper quartiles (error bars), and outliers (open circles above the error bars). Respondents in the tourism industry scored a higher SSAS for leopards, AWDs, and spotted hyenas.

Age: Respondent age did not correlate with their ability to correctly identify photos of any species or their SSASs, except that as age increased, respondents were better at identifying photos of striped hyenas (Kendall’s rank correlation, Z = 2.84, tau = 0.14, p = 0.005; Table 3-A1-1).

Table 3-A1-1: Results from Kendall's Rank Correlation tests, testing whether a respondent's ability to identify each species (left side of the table) or their SSAS for each species (right side) was correlated with age. As respondents' age increased, they became better at identifying striped hyenas. No correlations were found between age and SSASs for the six species.

Age						
	Species Identification			**SSAS**		
	Z =	**tau =**	**p =**	**Z =**	**tau =**	**p =**
Cheetah	-0.7	-0.04	0.49	0.24	0.01	0.81
Leopard	-0.51	-0.03	0.61	1.14	0.05	0.26
Lion	1.29	1.29	0.29	0.42	0.02	0.67
AWD	1.37	1.37	0.17	0.91	0.04	0.36
Spotted Hyena	-0.15	-0.15	0.88	-0.52	-0.02	0.61
Striped Hyena	2.84	2.84	0.005**	-0.79	-0.04	0.43

** Bonferroni corrections signifying a significant behavior change, $p \leq 0.01$.
* Bonferroni corrections signifying a suggestive behavior change, $0.05 \geq p > 0.01$.

Education: There was no correlation between a respondent's education level and ability to correctly identify photos of any species or their SSASs, except that as education increased, respondents were better at identifying photos of spotted hyenas (Z = 1.92, tau = 0.11, p = 0.05; Table 3-A1-2).

Table 3-A1-2: Results from Kendall's Rank Correlation tests, testing whether a respondent's ability to identify each species (left side of the table) or their SSAS for each species (right side) correlated with their education level. As education age increased, they were better at identifying spotted hyenas. No correlations were found between the six species' education levels and SSASs.

Education						
	Species Identification			**SSAS**		
	Z =	**tau =**	**p =**	**Z =**	**tau =**	**p =**
Cheetah	1	0.06	0.32	-1.01	-0.05	0.31
Leopard	0.78	0.78	0.43	-0.3	-0.01	0.76
Lion	-0.23	-0.01	0.82	0.36	0.02	0.72
AWD	1.8	0.1	0.07	-1.25	-0.06	0.21
Spotted Hyena	1.92	0.11	0.05*	-0.62	-0.03	0.53
Striped Hyena	0.06	0.003	0.95	-0.37	-0.02	0.71

* Bonferroni corrections signifying a suggestive behavior change, $0.05 \geq p > 0.01$.

Discussion

Perceptions: Leasing land to conservancies was the only socioeconomic variable associated with more positive SSASs for all six carnivore species (Figure 3-A1-4). This finding aligns with studies highlighting the correlation between conservancies or group-owned landscapes and more positive attitudes toward carnivores [14, 17-19]. Few studies, however, have demonstrated this influence across multiple species. Conservancies likely shape perceptions by providing benefits to landowners [57-59], such as access to critical livestock resources like grazing land and water during droughts [60]. Securing access to these resources has been linked to more positive attitudes and reduced intentions to kill lions [28], and our findings suggest this effect may extend to other carnivores. Additionally, monetary incentives for leasing land to a conservancy, such as payments for land use and supplementary income from employment or tourism, may also contribute to positive attitudes [5, 23, 29, 57, 58]. Over 90% of respondents ‘strongly agreed’ or ‘agreed’ that all six carnivore species were important for their family’s income or employment (Figure 3-4). Beyond financial benefits, conservancies may foster community ownership by enabling landowners to share wildlife-related costs and benefits [61]. These findings highlight the potential for conservancies to promote coexistence between people and carnivores. However, success depends on involving community members in land-use decisions and ensuring equitable cost-benefit distribution. Without this, conservancies risk fostering animosity toward decision-makers, conservationists, and wildlife, undermining their positive impact [28, 58, 62, 63].

Our results indicated that respondents from the ten original zones, where Lion Ambassadors (LAs) had been working for a year, had higher SSASs for all carnivore species except spotted hyenas compared to respondents from the five new zones, where LAs had recently started working (Figure 3-A1-2). A previous study in the Maasai Mara did not specifically measure perceptions and found fewer lions were killed when trusted community members warned others of their presence [44]. These findings suggest that LAs may positively influence perceptions and reduce anthropogenic mortality risk for these five species. Although predicting behavior from perceptions alone has limitations [9, 10], LAs may encourage more positive attitudes toward carnivores for several reasons. First, social factors, such as perceptions of what others in the community are doing about carnivores, can influence attitudes and intentions more than the actual costs imposed by carnivores [1, 5, 64]. As community members, LAs likely possess a deeper understanding of local values and beliefs, enabling them to promote coexistence effectively from a socially informed perspective [65, 66]. Second, hiring and educating local community members can empower them to participate in conservation initiatives and disseminate knowledge more broadly. Our results support this idea, as the presence of LAs was also associated with increased species identification proficiency. We recommend that conservation programs hire local community members to engage with their peers and participate in conservation efforts. Longitudinal surveys could provide stronger evidence of the relationship between LAs and perceptions. For example, tracking changes in SSASs among respondents in the five new zones over time could clarify how the duration of LA presence shapes perceptions of carnivores [64].

Pastoralists had lower SSASs than those working in tourism for leopards, AWDs, and spotted hyenas but not for cheetahs, lions, or striped hyenas (Figure 3-A1-8). This provides valuable species-specific insights complementing a previous MPCP survey, which found that livestock owners generally held lower attitudes toward all carnivores compared to those in tourism [23]. Expanding on this, we explore why pastoralists have lower SSASs for some species by examining responses to individual cost and benefit statements. Notably, nearly all respondents owned cattle (98%) and shoats (95%), including those in tourism, indicating widespread perception of livestock risks. More than half ‘strongly agreed’ that all carnivores pose significant risks to livestock (Figure 3-3), consistent with records of all six species killing livestock [32, 35, 37]. However, at least 7% more respondents ‘strongly agreed’ that lions and spotted hyenas posed greater risks than other species (Figure 3-3), suggesting both pastoralists and those in tourism view these species as particularly threatening. Despite this, pastoralists had lower SSASs for spotted hyenas than lions. Responses to benefit statements offer a possible explanation: 10–33% more respondents ‘strongly agreed’ with all four benefit statements for lions than for spotted hyenas, indicating that pastoralists likely associate fewer benefits with spotted hyenas (Figure 3-4). To address this, we recommend management interventions focus on reducing livestock risks posed by both species and increasing awareness of spotted hyenas' ecological and tourism-related benefits through targeted education campaigns.

Another interesting observation is that pastoralists had similar SSASs for cheetahs as those in the tourism industry (Figure 3-A1-8). This is noteworthy given that a similar percentage of respondents ‘strongly agreed’ that cheetahs (56%) posed a significant risk to their livestock as leopards (56%) and AWDs (57%), for which pastoralists had lower SSASs (Figure 3-4). This apparent contradiction can be clarified by examining responses to the cost and benefit statements. Notably, 12% of respondents were either ‘neutral,’ ‘disagreed,’ or ‘strongly disagreed’ that cheetahs posed a significant risk to their livestock (CS1), 6% more than the next closest species (Figure 3-4). This suggests pastoralists and those in tourism are more likely to view cheetahs as less threatening to livestock. These findings align with other studies reporting that cheetahs kill fewer livestock than other species [32, 35, 37], or being perceived as killing less [15, 52]. Moreover, while it’s reasonable to assume that those in the tourism industry are more likely to enjoy seeing cheetahs, the above observations may also explain why 7% more respondents ‘strongly agreed’ that they enjoy seeing cheetahs compared to the next closest species (Figure 3-5). The reduced perceived threat from cheetahs among pastoralists may make encounters less concerning, resulting in a more enjoyable experience.

Our results did not show that age or level of formal education was associated with differences in SSASs for each species (Tables 3-A1-1 & 3-A1-2). This is surprising given that previous studies have linked older age with lower attitudes and higher education with more positive attitudes toward carnivores [15, 29, 32, 67, 68]. One possible explanation may be the influence of unique factors in the Maasai Mara, such as benefits from leasing land to conservancies or working in the tourism industry. These benefits may be more evenly distributed across age groups and educational backgrounds, contributing to higher SSASs among a broader range of respondents. Additionally, as discussed earlier, Lion Ambassadors (LAs) may share knowledge about carnivores within their zones, fostering more positive perceptions even without formal education.

Species Identification: We found no socioeconomic variables significantly associated with respondents' ability to identify any of the six species. However, occupation appeared to have the most predictive power. Respondents working in the tourism industry were significantly more likely to correctly identify all three photos of leopards and striped hyenas than pastoralists (Figure 3-A1-7). Additionally, while not statistically significant, a higher percentage of those in the tourism industry correctly identified all three photos of cheetahs (95% to 83%), AWDs (75% to 59%), and spotted hyenas (93% to 81%). This may contradict a previous survey, which found that respondents who had lost livestock to carnivores were generally better at identifying species than other community members [32]. However, that survey did not compare those experiencing livestock losses to individuals in the tourism industry, who are more likely to receive specialized training and have extensive experience identifying carnivores. This suggests that greater exposure to carnivores, whether through tourism or livestock management, can enhance species identification skills. Those working in the tourism industry may have more direct experience with carnivores than pastoralists. However, both groups likely have more experience than other community members, which we did not survey. This is further supported by our overall findings, which show that most respondents, regardless of occupation, correctly identified all species except for striped hyenas, the rarest species in the Maasai Mara, with which most people have minimal direct experience.

A few socioeconomic and cultural variables were associated with respondents' ability to identify individual species. Respondents living in the ten original zones were more proficient at identifying striped hyenas than those in the five new zones. Additionally, though not statistically significant, a higher percentage of respondents from the original zones correctly identified all three photos of leopards (80% to 70%) and AWDs (64% to 56%). While previous studies have documented positive outcomes for carnivores when community members are employed in conservation roles [44], we are unaware of any study showing that their presence might also enhance the broader community’s ability to identify carnivores. Since LAs are employed by MPCP, an organization focused primarily on carnivore conservation, they are educated about carnivores and regularly engage in discussions about them. This likely leads to disseminating carnivore-related knowledge to other community members, potentially explaining the improved proficiency in species identification. However, since our data is correlative, future research could provide stronger evidence for this outcome, particularly through longitudinal survey designs that interview the same respondents over several time periods following the introduction of LAs [64].

Our results indicated that age and education were generally not associated with respondents' ability to identify most species (Tables 3-A1-1 & 3-A1-2). However, older respondents were more proficient at identifying striped hyenas (Table 3-A1-1). This may reflect greater exposure to the species, as anecdotal evidence from MPCP employees suggests striped hyenas were more common in the past. However, we lack concrete evidence to support this idea. Additionally, respondents with more formal education were better at identifying spotted hyenas. While a similar link between education and the ability to differentiate cheetahs and leopards has been reported [15], the specific reasons for this result with spotted hyenas remain unclear. Those with more education may have discussed spotted hyenas more often and, therefore, have more experience identifying them. However, if this were the case, we might also expect them to identify all or at least other species better. Given the limited research on this topic, we recommend future studies explore the relationship between age, education, and species identification to clarify why these factors may influence the ability to identify some species but not others.

Appendix 2: Comparisons between Species-Specific Attitude Scores (SSASs) within Respondents

Table 3-A2-1: Pairwise Comparisons of Species-Specific Attitude Scores (SSASs) across each species using within-subject, two-sample Wilcoxon signed-rank tests

Species	Median SSAS (Q1 to Q3)	Species Comparisons									
		Leopard		AWD		Lion		Striped Hyena		Spotted Hyena	
		V =	p =	V =	p =	V =	p =	V =	p =	V =	p =
Cheetah (n = 283)	+1 (-2 to +4)	15338	<0.01 **	18508	<0.01 **	17943	<0.01 **	26104	<0.01 **	29771	<0.01 **
Leopard (n = 282)	0 (-2 to +3)			15378	0.03*	16238	<0.01 **	22291	<0.01 **	28544	<0.01 **
AWD (n = 283)	0 (-3 to +3)					14244	0.06	18824	<0.01 **	25856	<0.01 **
Lion (n = 283)	0 (-3 to +2)							20182	<0.01 **	26526	<0.01 **
Striped Hyena (n = 283)	-2 (-5 to +2)									8294	<0.01 **
Spotted Hyena (n = 283)	-3 (-6 to 0)										

AWD refers to African wild dog

** Bonferroni corrections signifying a significant behavior change, p ≤ 0.01.

* Bonferroni corrections signifying a suggestive behavior change, 0.05 ≥ p > 0.01.

Appendix 3: Comparison of Species Identification Ability within Respondents

Table 3-A3-1: Pairwise comparisons of individual ability to identify all three photos of each species using within-subject, two-sample Wilcoxon signed-rank tests.

Species	**Correct Ident.** (n) / **Misident.** (n)	**Species Comparisons**									
		Cheetah		**Spotted Hyena**		**Leopard**		**AWD**		**Striped Hyena**	
		V =	p =	V =	p =	V =	p =	V =	p =	V =	p =
Lion (n = 283)	276 / 7	1097	<0.01 **	1301	<0.01 **	2274	<0.01 **	5431	<0.01 **	14093	<0.01 **
Cheetah (n = 283)	239 / 44			1101	0.63	1958	<0.01 **	6035	<0.01 **	13074	<0.01 **
Spotted Hyena (n = 283)	233 / 50					2238	<0.01 **	6072	<0.01 **	12426	<0.01 **
Leopard (n = 282)	219 / 63							5719	<0.01 **	11969	<0.01 **
AWD (n = 283)	175 / 108									9094	<0.01 **
Striped Hyena (n = 282)	113 / 169										

Corrent Ident. (n) / Misident (n) refers to the number of respondents who correctly identified all three photos and number who misidentified one or more photos of that species.

** Bonferroni corrections signifying a significant behavior change, $p \leq 0.01$.

* Bonferroni corrections signifying a suggestive behavior change, $0.05 \geq p > 0.01$.

Table 3-A3-2: Pairwise comparisons of individual ability to correctly identify each of the three photos for each species using within-subject, two-sample signed-rank tests.

Species	**Photo Comparisons** (n of misidentifications)	**Flank**		**Head-on**	
		V =	**p =**	**V =**	**p =**
Lion	Flank (n = 2)				
	Head-on (n = 2)	1.5	1		
	Lying-down (n = 6)	17.5	0.13	10	0.07
Cheetah	Flank (n = 14)				
	Head-on (n = 26)	326	0.03*		
	Lying-down (n = 17)	210	0.57	150	0.1
Spotted Hyena	Flank (n = 7)				
	Head-on (n = 12)	99	0.24		
	Lying-down (n = 33)	677	<0.001**	704	0.001**
Leopard	Flank (n = 26)				
	Head-on (n = 37)	644	0.1		
	Lying-down (n = 30)	440	0.43	192	0.21
AWD	Flank (n = 36)				
	Head-on (n = 78)	1556	<0.001**		
	Lying-down (n = 66)	833	<0.001**	845	0.13
Striped Hyena	Flank (n = 72)				
	Head-on (n = 95)	4233	<0.001**		
	Lying-down (n = 137)	1376	0.004**	1024	<0.001**

** Bonferroni corrections signifying a significant behavior change, $p \leq 0.01$.
* Bonferroni corrections signifying a suggestive behavior change, $0.05 \geq p > 0.01$.

Appendix 4: Survey Instrument

Survey Instrument *(English version, contact the authors for the Ma version)*

Before commencing with the interview, please ask the person you are interviewing whether they are giving you permission to conduct the interview.

Has the person granted you permission to conduct the interview? ☐ Yes ☐ No

Background

1. What age set are you in? ☐ Irenchaai ☐ Ilmeshuki ☐ Ilkishili ☐ Ilkirupi
   ☐ Irrampauni ☐ Iltiyiogoni ☐ Ilterekeyiani ☐ Ilnyangusi
2. What is your education level? ☐ None ☐ Primary ☐ Secondary
   ☐ Tertiary
3. What is your main occupation? ☐ Pastoralist ☐ Agriculturist ☐ Businessman
   ☐ Employed in the tourism sector
   ☐ Other ________________
4. What religion do you adhere to? ☐ Christianity ☐ Muslim ☐ Traditional
   ☐ Other: _______________
5. Do you own any cattle? ☐ Yes ☐ No
   a. If yes, How many cattle do you own? __________
6. Do you own any shoats? ☐ Yes ☐ No
   a. If yes, How many shoats do you own? _________
7. Do you lease land to a conservancy? ☐ Yes ☐ No
   a. If yes, Which conservancy? ____________

Species Identification

1. **1.** Species Photos

Lion Flank:

© Brian Schuh

Lion Head-on:

© Unknown

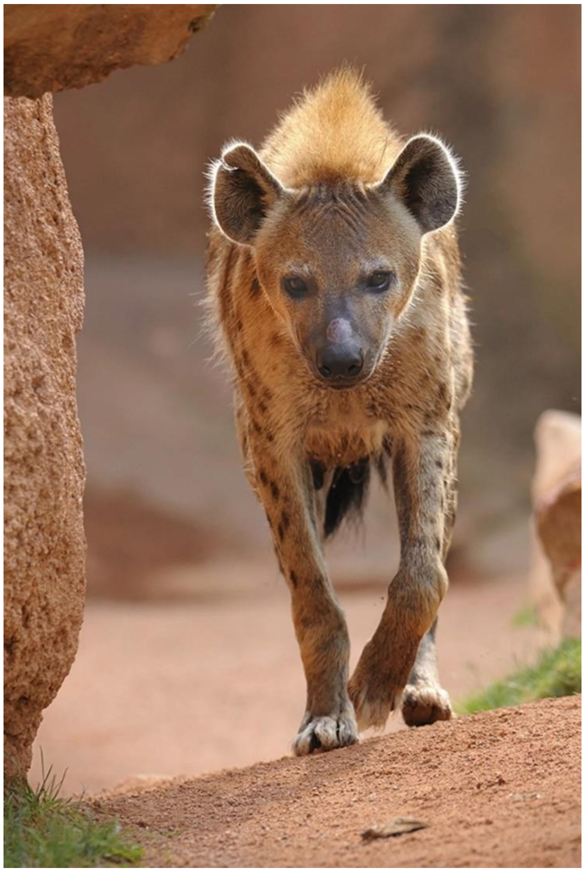
Lion Lying Down:

© Big Stock Images

Spotted Hyena Fank:

© Unknown

Spotted Hyena Head-on:



© Nat Geo Kids

Spotted Hyena Lying Down:

© Brian Schuh

Cheetah Flank:

© Brian Schuh

Cheetah Head-On:

© Brian Schuh

Cheetah Lying Down:

© Brian Schuh

Leopard Flank:

© Lonely Planet

Leopard Head-on:

© Travel and Leisure

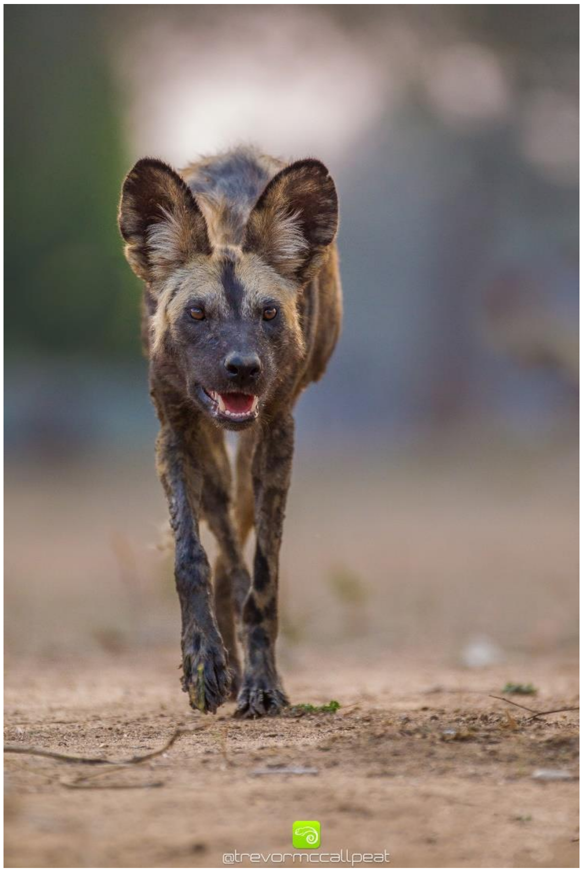
Leopard Lying Down:

© Unknown

African wild dog Flank:

© Brian Schuh

African wild dog Head-on:



© @trevormccallpeat

African wild dog Lying Down:

© Unknown

Striped Hyena Flank:

© RoundGlassSustain

Striped Hyena Head-on:

© @jitenderdavyaal580

Striped Hyena Lying Down:

© @cari_rhsc

2. Procedure

- **a.** Without looking, select a single laminated card from ‘Randomization Card Set 1’.
- **b.** Show the respondent the photo corresponding to the card you selected from ‘Set 1,’ and ask them: English: “What animal do you see in this photo?” / Maa: “Kaa ngures ena natii ena pisha?”
- **c.** Record the respondent's answer in Cybertracker.
- **d.** Place the used card in a secure place, not back into the ‘Set 1’ folder.
- **e.** Repeat sets a – d until you have shown all 18

Animal (English/Maa)	**Picture**	**What species did the respondent ID this picture as?**
Cheetah/Olowuaru keri	Flank	
	Head-on	
	Lying down	
Leopard/Olkinya lasho	Flank	
	Head-on	
	Lying down	
Lion/Olngatuny	Flank	
	Head-on	
	Lying down	
African wild dog/Osuyiani	Flank	
	Head-on	
	Lying down	
Spotted Hyena/Orkonoi	Flank	
	Head-on	
	Lying down	
Striped Hyena/Nesompori	Flank	
	Head-on	
	Lying down	

3. Randomized Card Set 1

1 **Cheetah: Flank**	**2** **Cheetah: Head-on**	**3** **Cheetah: Lying**
4 **Lion: Flank**	**5** **Lion: Head-on**	**6** **Lion: Lying**
7 **Leopard: Flank**	**8** **Leopard: Head-on**	**9** **Leopard: Lying**
10 **African Wild Dog: Flank**	**11** **African Wild Dog: Head-on**	**12** **African Wild Dog: Lying**
13 **Spotted Hyena: Flank**	**14** **Spotted Hyena: Head-on**	**15** **Spotted Hyena: Lying**
16 **Striped Hyena: Flank**	**17** **Striped Hyena: Head-on**	**18** **Striped Hyena: Lying**

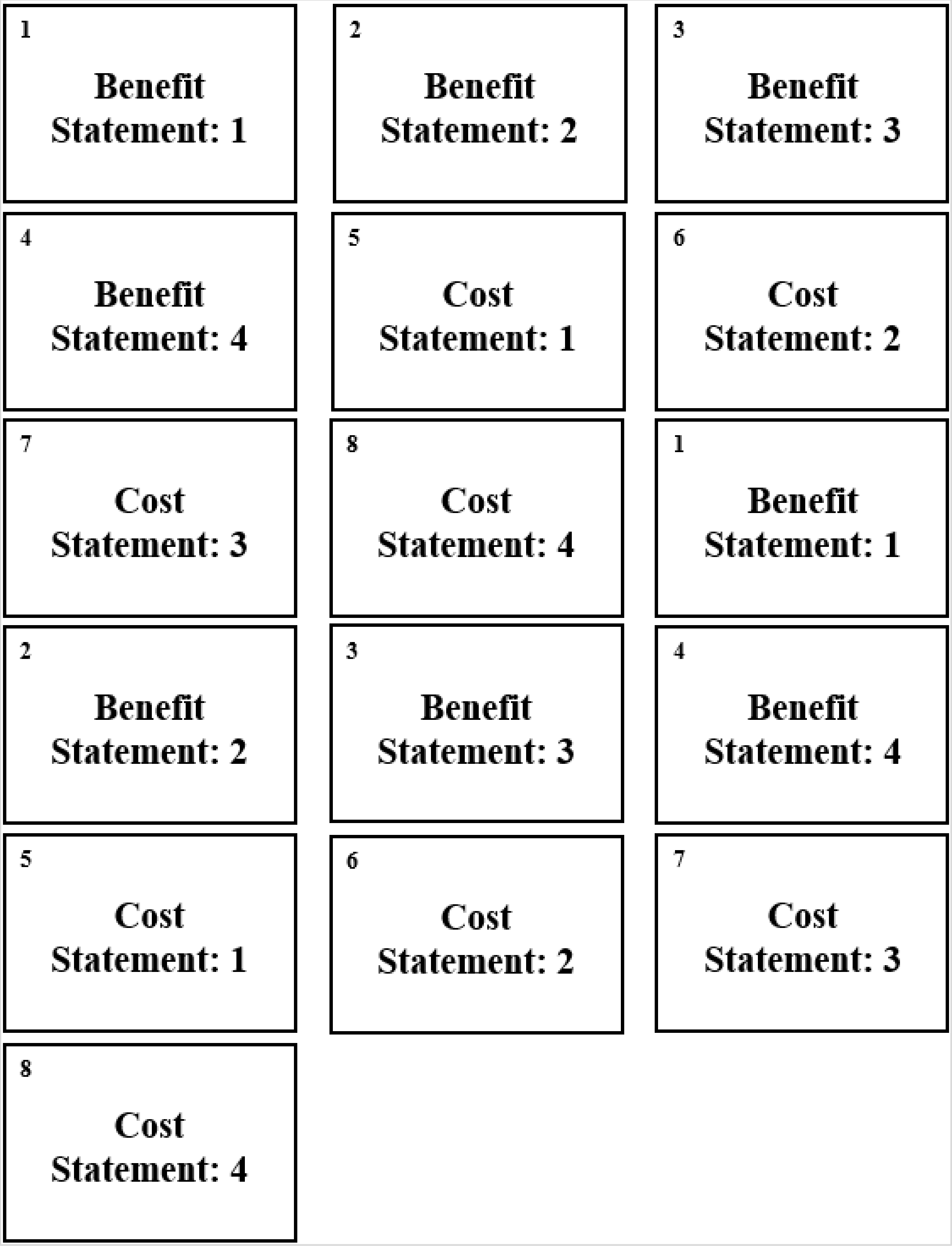
Species-Specific Perceptions

1. Propose each of the eight statements below to the respondent for a single carnivore species before moving onto the next species.
    - a. Use ‘Set 1’ cards to randomly chose the order of carnivore species for each interview.
    - b. Use ‘Set 2’ cards to randomly chose the order of statement for each species.
    - c. Explain the five potential responses for each statement and clearly describe how each response is different. Layout the face card and define each to a specific response (Strongly agree = big smile, agree = little smile, neutral = neutral face, disagree = little frown, strongly disagree = angry face).

Benefit Statements (English/Maa)	Strongly Agree	Agree	Neutral	Disagree	Strongly Disagree
“I think seeing (cheetahs, leopards, lions, AWDs, spotted/striped hyenas) is enjoyable.” “Ore pee idol (Olowuaru keri, Olkinya lasho, Olngatuny, Osuyiani, Orkonoi, Nesompori) naa entoki sidai keshipakino nkonyek.”	5	4	3	2	1
“I think (cheetahs, leopards, lions, AWDs, spotted/striped hyenas) play an important role to maintain a healthy ecosystem.” “Ore (Olowuaru keri, Olkinya lasho, Olngatuny, Osuyiani, Orkonoi, Nesompori) naa keeta tipat tolmanyara.”	5	4	3	2	1
“I think (cheetahs, leopards, lions, AWDs, spotted/striped hyenas) are important to me and my family's employment or income.” “Kojo ore (Olowuaru keri, Olkinya lasho, Olngatuny, Osuyiani, Orkonoi, Nesompori) naa keeti tipat tialo ten anu olmarei lai tialo ilkasin o ropiyiani.”	5	4	3	2	1
“I think (cheetahs, leopards, lions, AWDs, stopped/striped hyenas) are important to tourism.” “ Kajo ore (Olowuaru keri, Olkinya lasho, Olngatuny, Osuyiani, Orkonoi, Nesompori) naa ile tipod tesiaai olashumpai epuonu enakop.”	5	4	3	2	1
Costs Statements (English/Maa)					
“I think (cheetahs, leopards, lions, AWDs, spotted/striped hyenas) pose a significant risk to my livestock.” “Kajo ore (Olowuaru keri, Olkinya lasho, Olngatuny, Osuyiani, Orkonoi, Nesompori) naa keyau batisho tialo nkishu o ntare ainei.”	-5	-4	-3	-2	-1

"I think (cheetahs, leopards, lions, AWDs, spotted/striped hyenas) pose a significant risk to other people's livestock." "Kajo ore (Olowuaru keri, Olkinya lasho, Olngatuny, Osuyiani, Orkonoi, Nesompori) naa keyau batisho tialo nkishu o ntare o kulikae tung ana."	-5	-4	-3	-2	-1
"I think (cheetahs, leopards, lions, AWDs, spotted/striped hyenas) pose a significant risk to me or my family." Kajo ore (Olowuaru keri, Olkinya lasho, Olngatuny, Osuyiani, Orkonoi, Nesompori) naa keyau batisho tialo enkishui olmarei lai."	-5	-4	-3	-2	-1
"I think (cheetahs, leopards, lions, AWDs, spotted/striped hyenas) pose a significant risk to other people in the community." "Kajo ore (Olowuaru keri, Olkinya lasho, Olngatuny, Osuyiani, Orkonoi, Nesompori) naa keyau batisho tenkishui e kulikae lelatia."	-5	-4	-3	-2	-1

2. Randomization Card Set 2



1 **Benefit Statement: 1**	2 **Benefit Statement: 2**	3 **Benefit Statement: 3**
4 **Benefit Statement: 4**	5 **Cost Statement: 1**	6 **Cost Statement: 2**
7 **Cost Statement: 3**	8 **Cost Statement: 4**	1 **Benefit Statement: 1**
2 **Benefit Statement: 2**	3 **Benefit Statement: 3**	4 **Benefit Statement: 4**
5 **Cost Statement: 1**	6 **Cost Statement: 2**	7 **Cost Statement: 3**
8 **Cost Statement: 4**		

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Conclusion:

Across three chapters, this dissertation examines the short-term responses of cheetahs to two types of livestock and domestic dog breeds, and investigates the relationship between people's perceptions of multiple native carnivore species and their ability to identify each. Together, these studies contribute to an interdisciplinary understanding of how human-associated stimuli influence carnivore behavior, the risks carnivores pose to people, and the risks people pose to carnivores. By integrating behavioral and social dimensions, the results inform management interventions that protect people's livelihoods and carnivores.

Chapter 1 demonstrated that cattle vocalizations deterred some cheetahs, causing movement away from the stimulus. This weak evidence for deterrence suggests that interactions with cattle can lead to short-term displacement, potentially altering movement, increasing stress, reducing reproductive success, or causing habitat exclusion if interactions are frequent. In contrast, few cheetahs moved after the shoat playback, providing no evidence for deterrence or attraction. Thus, the presence of shoats is unlikely to cause significant behavioral changes but may instead influence cheetahs indirectly through habitat modification or prey availability. These findings underscore the need for livestock managers to minimize the indirect effects of livestock presence while considering the frequency of cheetah-cattle interactions to reduce the risk of displacing individuals.

Chapter 2 examined how cheetahs respond to vocalizations from different breeds of domestic dogs. Livestock guarding dogs (LGDs) elicited movement away from the playback speaker in nearly half of the individuals, providing limited evidence of deterrence. In contrast, village dogs (VDs) elicited minimal responses, offering no support for deterrence or attraction. These findings highlight the potential for LGDs to protect livestock by directly deterring cheetahs but also reveal significant variability in individual responses. Reduced livestock losses associated with LGDs may be partially attributed to their ability to alert humans, who can intervene. Conversely, village dogs, despite their limited immediate impact on cheetah behavior, may indirectly affect carnivores through competition for prey or disease transmission. Therefore, regulating village dog populations is essential to promoting coexistence in shared landscapes.

Chapter 3 investigated the relationship between species-specific perceptions and identification ability among community members living near Kenya's Maasai Mara National Reserve. Results showed strong support for species-specific perceptions across most carnivores, with some evidence of misapplied perceptions among individuals prone to species confusion. For example, respondents who misidentified photos of spotted hyenas as cheetahs appeared to misapply positive perceptions of cheetahs onto hyenas, while those who misidentified photos of African wild dogs as spotted hyenas appeared to misapply negative perceptions of hyenas onto wild dogs. These findings indicate that individuals perceive distinct costs and benefits from different species, likely contributing to variations in attitudes and behaviors. This underscores the importance of measuring species-specific attitudes, as both the risk of anthropogenic mortality and the effectiveness of management interventions will likely vary by species. Furthermore, assessments of identification ability should be included in such studies, as misidentification may shape attitudes toward certain carnivores, especially among individuals prone to species confusion.

Collectively, these studies emphasize the value of direct, experimental approaches for understanding carnivore responses to human-associated stimuli and the variability among individual carnivores. Future research should expand these frameworks to additional carnivore species, examine how group characteristics (e.g., males versus females or single individuals versus mothers with cubs) influence responses and investigate the long-term impacts of deterrent effects like those observed with cattle and LGDs. Tracking the movement of carnivores and livestock simultaneously using high-resolution GPS could provide detailed insights into when and where interactions occur and how these interactions affect carnivore behavior. Similarly, refining methodologies to assess species confusion and its influence on perceptions would improve predictions of human behavior toward carnivores and inform interventions. Through this interdisciplinary research, we aim to inform management interventions that address the drivers of human-carnivore conflict. By integrating findings on livestock, domestic dogs, and species-specific perceptions, this dissertation provides actionable insights to mitigate conflict, protect livelihoods, and support the long-term conservation of carnivore populations. These results reinforce the need for collaborative, evidence-based approaches to promote coexistence in human-dominated landscapes.