Original Article

Hierarchy of fear: experimentally testing ungulate reactions to lion, African wild dog and cheetah

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Experiments have begun demonstrating that the fear (antipredator behavioral responses) large carnivores inspire in ungulates can shape ecosystem structure and function. Most such experiments have focused on the impacts of either just one large carnivore, or all as a whole, rather than the different impacts different large carnivores may have in intact multi-predator-prey systems. Experimentally testing the relative fearfulness ungulates demonstrate toward different large carnivores is a necessary first step in addressing these likely differing impacts. We tested the fearfulness ungulates demonstrated to playbacks of lion (*Panthera leo*), African wild dog (*Lycaon pictus*), cheetah (*Acinonyx jubatus*) or non-predator control (bird) vocalizations, in Greater Kruger National Park, South Africa. Ungulates ran most to lions, then wild dogs, and then cheetahs, demonstrating a very clear hierarchy of fear. Those that did not run looked toward the sound more on hearing large carnivores than controls, looking most on hearing lions. Notably, prey species-specific population level kill rates by each predator did not predict the patterns observed. Our results demonstrate that different large carnivores inspire different levels of fear in their ungulate prey, pointing to differing community-level impacts, which we discuss in relation to the ongoing worldwide decline and loss of large carnivores.

Key words: **antipredator behavior, ecology of fear, large carnivore, multi-predator-prey systems, perceived predation risk.**

INTRODUCTION

Large carnivores have dramatically declined in number and range worldwide (Ripple et al. 2014; Wolf and Ripple 2017) creating "natural experiments" that point to their essential role in shaping ecosystem structure and function (Estes et al. 2011; Ripple et al. 2014). Declines have been most dramatic in Africa as evidenced by lion (*Panthera leo*), African wild dog (*Lycaon pictus*), and cheetah (*Acinonyx jubatus*) comprising half of the six large carnivore species globally with the greatest range contractions (Bauer et al. 2015; Wolf and Ripple 2017). Recent manipulative experiments, mainly involving African ungulates, have begun demonstrating that the fear (antipredator behavioral responses; Zanette and Clinchy 2020)

that large carnivores inspire in ungulates and mesocarnivores can cause powerful trophic cascades and restructure ecosystems at the community level (Ford et al. 2014; Suraci et al. 2016; le Roux et al. 2018; Atkins et al. 2019; Zanette and Clinchy 2020). Other recent experiments testing the antipredator responses of many different African ungulates to playbacks of large carnivore vocalizations suggest that these community-level impacts could be commonplace (McComb et al. 2011; van der Meer et al. 2012, 2015; Favreau et al. 2013; Dalerum and Belton 2015; Dannock et al. 2019; Makin et al. 2019). A limitation of most such experiments has been that antipredator responses to only a single large carnivore are tested in any given study. This constrains our understanding of most intact large carnivore-ungulate communities, which generally function as multi-predator-prey systems (Thaker et al. 2011; Say-Sallaz et al. 2019; Pays et al. 2020).

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Table 1

Species recorded, number of videos of each, and each predator's prey preferences

| Species name | | | Predator's prey preferences | | | |
| Common | Latin | | Jacobs' Index (JI) values | | | |
		Videos	Lion[a]	Lion[b]	Wild dog[b]	Cheetah[b]
Ungulates						
Impala	*Aepyceros melampus*	391	−0.93	−0.73	+0.25	+0.11
Warthog	*Phacochoerus africanus*	83	+0.38	+0.11	−0.52	−0.41
Elephant	*Loxodonta africana*	46	−1.00	−0.87	−1.00	−1.00
Zebra	*Equus quagga*	37	+0.50	+0.16	−0.88	−0.69
Duiker	*Sylvicapra grimmia*	32		−0.83	+0.15	+0.18
Giraffe	*Giraffa camelopardalis*	24	+0.81	+0.24	−1.00	−0.95
White rhino	*Ceratotherium simum*	23	−0.39	−1.00	−1.00	−1.00
Steenbok	*Raphicerus campestris*	16		−0.86	−0.34	−0.02
Kudu	*Tragelaphus strepsiceros*	14	−0.37	+0.13	+0.35	−0.04
Hippo	*Hippopotamus amphibius*	8		−0.45	−1.00	−1.00
Nyala	*Tragelaphus angasi*	2		−0.32	−0.48	−0.58
Buffalo	*Syncerus caffer*	1	+0.60	+0.32	−0.98	−0.98
Large carnivores						
Hyena	*Crocuta crocuta*	85				
Leopard	*Panthera pardus*	13				
Lion	*Panthera leo*	5				

[a]Data from de Boer et al. (2010), collected at our study site (Klaserie).
[b]Data from Clements et al. (2014), a review of 45 studies from across Africa.

Community ecologists have traditionally tended to treat predators as a single, homogeneous trophic level (Fretwell 1987) with different species of predators being viewed as functionally interchangeable in the effects they exert on prey (Chalcraft and Resetarits 2003; Schmitz 2007). This perspective is changing, with ever more authors now proposing that predator identity matters, and that the presence or absence of multiple predators (i.e., predator diversity) could lead to substantially different community-wide effects on herbivore reproduction, mesopredator suppression, and alterations in plant species richness (Ives et al. 2005; Schmitz 2007; Finke and Snyder 2010; Say-Sallaz et al. 2019). Consequently, predators may thus have a mosaic of distinct, interacting impacts with singular and interactive consequences on ecosystem functions (Schmitz 2007; Griffin et al. 2015; Pays et al. 2020; Resetarits et al. 2021). As such, prey may be expected to adjust their fear responses relative to each predator and the danger that predator represents (Schmitz 2007; Say-Sallaz et al. 2019; Epperly et al. 2021; Palmer and Packer 2021). An increasing number of correlative studies have begun investigating the impacts of multiple large carnivores simultaneously (Thaker et al. 2011; Creel et al. 2017, 2019; Dröge et al. 2017; Makin et al. 2017; Say-Sallaz et al. 2019; Pays et al. 2020), but there remains little direct experimental evidence regarding the fear effects that multiple large carnivores exert in the ungulate community as a whole (Zanette and Clinchy 2020; Epperly et al. 2021; Palmer and Packer 2021).

Experimental testing is essential to further our understanding of multi-predator fear effects in large carnivore-ungulate systems as there is presently no certain means to predict which large carnivore is feared most by their prey (Zanette and Clinchy 2020; Palmer and Packer 2021). There is growing evidence of the complexity of what cognitively sophisticated species like birds and mammals find fearful (Zanette and Clinchy 2020), and many competing ideas exist concerning what most strongly mediates fear (Palmer and Packer 2021). The most commonly proposed hypothesis is that selection

should favor antipredator responses that correlate positively with predation rates (Creel and Christianson 2008; Creel et al. 2019), that is, prey should most fear the predator that causes the greatest mortality among them. Yet, the increasing number of correlative studies that have explored the fear responses of ungulates to multiple large carnivores have found that the strength of antipredator strategies does not correlate with species-specific kill rates (Thaker et al. 2011; Creel et al. 2017, 2019; Dröge et al. 2017; Makin et al. 2017; Packer and Palmer 2021). Kill rates to some degree reflect the predator's choice of what to attempt to attack and kill, and hence the predator's perspective (Creel et al. 2019; Palmer and Packer 2021). From the individual prey's perspective, it may not be the per capita kill rate in the population but the likelihood of being killed if a given predator decides to attack which predominantly determines which predator elicits the strongest fear response (Bouskila and Blumstein 1992; Creel 2018; Creel et al. 2019; Palmer and Packer 2021).

Lions, African wild dogs, and cheetahs have been included in each of the several recent correlative studies that have compared the responses of African ungulates to multiple large carnivores (Thaker et al. 2011; Creel et al. 2017, 2019; Dröge et al. 2017; Makin et al. 2017; Pays et al. 2020). Manipulative experiments have also been conducted which have separately tested the reactions of ungulates to playbacks of lions (McComb et al. 2011; Favreau et al. 2013; Dalerum and Belton 2015; Dannock et al. 2019; Makin et al. 2019) or wild dogs (van der Meer et al. 2012, 2015), but there has been no experiment to date directly comparing the fear responses of ungulates to hearing lions or wild dogs at the same study site; and to the best of our knowledge no prior experiment has yet tested ungulate responses to cheetah vocalizations. Lions, wild dogs, and cheetah have distinct prey preferences (gauged using Jacob's index [J.I.]: % of predator's kills comprised of species x/% of prey individuals in the environment comprised of species x; Clements et al. 2014), with lions preferring to kill larger ungulates like giraffe

and buffalo whereas wild dogs and cheetah prefer smaller prey such as impala (Table 1). Lions, being both large (180 kg) and group hunters, are capable of killing any prey they encounter, from elephants (1600 kg) to steenbok (8 kg; Périquet et al. 2015; Table 1). Cheetahs are larger than wild dogs (45 vs. 25 kg respectively) but because wild dogs hunt in packs whereas cheetahs hunt singularly or in very small groups wild dogs more commonly kill larger prey than cheetahs do (Creel et al. 2017; Table 1).

Experimentally establishing whether some large carnivores inspire more fear than others is a necessary first step in determining the community-level impacts of fear in systems with multiple large carnivores, and can inform conservation plans by helping to identify the potential consequences of the decline or recovery of one large carnivore versus another (Schmitz 2007; Heithaus et al. 2008; Clinchy et al. 2016; Say-Sallaz et al. 2019; Pays et al. 2020; Palmer and Packer 2021). To accomplish this essential step, we experimentally tested the relative fearfulness ungulates demonstrated in reaction to hearing vocalizations of lions, African wild dogs, cheetahs, or non-predator controls (birds) in Greater Kruger National Park, South Africa. This study area offered an intact system where all three large carnivores persist in reasonable numbers (Marnewick et al. 2014; Bauer et al. 2015) and the prey preferences of each are well-documented (de Boer et al. 2010; Clements et al. 2014; Maruping-Mzileni et al. 2017). Our experimental procedure additionally provided the opportunity to record the reactions of both ungulates and large carnivores themselves to the perceived presence of multiple large carnivores, and we report the similarities and contrasts in their responses.

We tested three hypotheses: 1) no large carnivore is feared more than another, consistent with traditional assumptions in community ecology (Schmitz 2007); 2) fear varies with the species-specific kill rate, as most commonly hypothesized (Creel and Christianson 2008); and 3) fear varies with the likelihood of being killed if the given large carnivore decides to attack (Bouskila and Blumstein 1992; Creel 2018; Palmer and Packer 2021). Three distinct corresponding predictions follow which are respectively that: 1) all species respond more to large carnivores than controls but not more to one large carnivore than another; 2) species differ in their responses with each species most fearing the large carnivore that causes the greatest mortality among them; and 3) all species should most fear lions, followed by African wild dogs and then cheetahs, given that the larger and more social the large carnivore the more certain it is to cause death if it decides to attack (Bouskila and Blumstein 1992; Adams 2003; Benson-Amram et al. 2017; Černý et al. 2019). We discuss the implications of our results in relation to the likely community-level impacts of multiple predator effects, and to the potential mediators of fear in large carnivore-ungulate systems.

METHODS

Overview and study site

We experimentally tested the reactions of both ungulates and large carnivores to playbacks of the vocalizations of lions, African wild dogs, cheetahs, and non-predator controls (birds), following a well-established experimental protocol (Smith et al. 2017; Suraci et al. 2017a, 2017b, 2019b; Epperly et al. 2021; Crawford et al. 2022; Widén et al. 2022). Trials were performed at 14 sites (a median of 2.6 km apart) from 7-30 July 2017 in the Klaserie Private Nature Reserve (24.203S, 31.179E), which is part of the Greater Kruger National Park (Child et al. 2013).

Broadcasting predator vocalizations has proved to be a particularly effective means of inducing fear in the growing number of experiments demonstrating that antipredator responses can have population-, community- and ecosystem-level impacts in free-living wildlife (e.g., Zanette et al. 2011; Suraci et al. 2016; Smith et al. 2017; Atkins et al. 2019; Suraci et al. 2019a; Allen et al. 2022). The general applicability of this approach was corroborated in a review by Hettena et al. (2014). These authors identified 183 predator playback experiments, 154 of which were on mammals, and their analysis confirmed that in the great majority of these experiments not only did prey recognize their predator`s vocalizations, hearing their predator's vocalizations reliably induced antipredator responses powerful enough to be anticipated to have population-, community- and ecosystem-level impacts.

Lion vocalizations consisted of snarls and growls (shorter distance sounds made during mating or aggression, not long distance calls like roars; Makin et al. 2019), wild dog vocalizations were comprised of "twitter" and "hoo" calls (shorter and medium distance contact calls respectively; Webster et al. 2010) and those of cheetahs were shorter distance sounds related to courting or aggression (Smirnova et al. 2016). To comprise an optimal, non-threatening control composed of familiar, benign heterospecific animal vocalizations (Hettena et al. 2014), we used the vocalizations of three locally abundant species of birds, the African Hoopoe (*Upupa africana*), Pearl-Spotted Owlet (*Glaucidium perlatum*), and African Wood Owl (*Strix woodfordi*), broadcast during diel, crepuscular, and nocturnal hours, respectively. We designed avian vocalizations to constitute a single treatment (controls) and treated them as such in our analyses (Zanette et al. 2011; Epperly et al. 2021; Crawford et al. 2022; Widén et al. 2022). We used multiple (≥7) exemplars of representative vocalizations of each large carnivore and the controls. We recorded reactions to playbacks using Automated Behavioral Response (ABR) systems, which are video-enabled camera traps linked to playback units triggered by the camera's activation (Suraci et al. 2017a). Playbacks were standardized to a volume of 80 dB at 1 m; loud enough to be audible, but not startling, for animals within the 15 m detection range of the camera's motion sensor (Smith et al. 2017; Suraci et al. 2017a, 2017b, 2019b; Epperly et al. 2021; Crawford et al. 2022). The vocalizations chosen were also selected for this reason, that is, likely to be heard at this decibel level at this 15 m range, in contrast to, for example, lion roars, which are emitted at a much higher decibel level (Makin et al. 2019).

Experimental design and behavioral measures

One ABR was deployed at each site, attached to a tree, with the camera positioned at a height of 1.5 m and the connected speaker 0.5 m directly above. Video recording began immediately after the camera was triggered by animal motion, and a 3-second delay was set before the speaker broadcast a 10-s playback. Prior ABR experiments have established that this short delay is sufficient to identify a change in behavior in reaction to the playback, for example, a walking animal runs, or a foraging animal looks toward the sound, demonstrating it is reacting directly to the sound (Suraci et al. 2017a, 2017b; Epperly et al. 2021). Quantification of reactions was then restricted to individuals visible in the video both before and after the playback began.

We focused on three reactions: Running, Look toward Sound, and Approaching. Running was operationally defined as taking more than 3 consecutive rapid steps; Look toward Sound entailed orienting directly toward the speaker with head up and both eyes

and both ears visible to the camera (just 0.5 m directly below the speaker); and Approaching comprised walking toward the speaker with head up and both eyes and both ears visible to the camera. These three reactions are readily recognizable in each of the diverse species we recorded, whereas operational definitions of other behaviors applicable across species quickly become cumbersome, for example, "prolonged listening" has been used to quantify the responses of elephants to lion playbacks (McComb et al. 2011) but is difficult to recognize in other species. Animals performing any of the three behaviors we quantified before the playback began (e.g., Running before) were omitted from analyses, ensuring that all reactions were due to the playback treatment. We first considered whether or not an animal Ran to a playback. Of animals that did not Run, we then examined whether they Looked toward the Sound and/or Approached. If more than one individual of a species was in view, we quantified the reactions of up to the nearest five and took their median response as representative of the reaction in that video (Dalerum and Belton 2015; Epperly et al. 2021).

Every ABR was programmed to operate over the entire 24-h diel cycle. We ensured potential exposure to each treatment was balanced across the 24 h: if the ABR was triggered during a given hour (e.g., 12:00 to 01:00 AM) one treatment would play (e.g., lions), and in the next hour (01:00 to 02:00 AM) a different treatment would play (e.g., wild dogs), up until all four had been played. The process was then repeated with the sequence within each 4-h block randomly organized to avoid order effects, and exemplars randomly selected within each hour to avoid pseudo-replication (Epperly et al. 2021; Crawford et al. 2022). If an animal remained in front of the ABR after the first time it heard a playback, and thus re-triggered the system, it would hear another playback, which would most likely be of the same treatment as the first given the ABRs were programmed to broadcast the same treatment throughout a given hour on the clock. Repeated exposures to the same treatment within an hour cannot be considered independent and we accordingly classified each exposure as to whether it was a "first" or "repeat" within an hour and included this in our statistical analyses (Suraci et al. 2017b; Epperly et al. 2021; Crawford et al. 2022). The 'first" plus any and all "repeat" exposure videos within an hour we defined as a "bout" (Widén et al. 2022), and we assigned a number to each to distinguish "bout identity".

We classified all three responses as yes/no binary variables, providing one data point per behavioral category per video (Smith et al. 2017; Suraci et al. 2017a, 2017b, 2019b; Epperly et al. 2021; Crawford et al. 2022). This straightforward binomial classification ensured high inter-observer reliability (verified by preliminary testing performed among three of the authors). One individual was thus able to score all the videos with no apparent bias, which was further ensured by their doing so while "blind" to the treatment (i.e., with audio muted).

Statistical analyses

To test the effect of playback treatment on Running and Approaching, we fit both response variables using binomial generalized linear mixed models (GLMMs) with a logit link, with playback treatment and exposure (whether "first" or "repeat" videos) as predictor variables, incorporating "bout identity" and camera site as random effects. GLMMs concerning Look toward Sound did not converge so we instead used semi-parametric logit link Generalized Estimating Equations (GEEs) with an exchangeable covariance structure and individual as the correlation structure (Fieberg et al.

2009; Koper and Manseau 2009) to test for effects on Look toward Sound (for on overview see Supplementary Materials Table S1).

We quantified the reactions of 12 species of ungulates and 3 species of large carnivores (Table 1). Considering Running by ungulates first, we began by testing the effect of playback treatment on Running using pooled data from all the ungulates. Next, we subdivided the ungulates into three components each comprised of a sufficient sample size ($N > 80$ videos) to meaningfully test, and analyzed the effect of playback treatment on Running in impalas, warthogs, and all other ungulates excluding impala and warthog (Table 1). Considering Look toward Sound, we first tested the effect of playback treatment using pooled data from all the ungulates, and then tested the effect in impalas alone. As noted above, Looked toward Sound was only scored for animals that did not Run, meaning the sample size was smaller than when testing Running, and for this reason and convergence issues we were unable to separate out the responses of anything but impala. In the case of Approaching, ungulates did this so rarely ($N = 4$ instances; 0 impala, 1 warthog, 3 other), species-specific analyses were infeasible. Turning to contrasting the responses to the playback treatments of ungulates versus large carnivores themselves, we included "guild" (ungulate or carnivore) as a third predictor and tested the effects on all of Running, Look toward Sound, and Approach. Finally, we considered the responses of large carnivores alone, pooling all the available videos of them. There were too few videos of large carnivores Running to conduct analyses, but there were enough to test for effects on Look toward Sound and Approaching contrasting responses to controls versus the pooled reactions to any large carnivore playback (i.e., lion, wild dog, and cheetah playbacks combined).

For all models, we report Wald's χ^2 test statistic (Bolker et al. 2009), followed by Holm-Bonferroni post-hoc tests where necessary (Holm 1979). All analyses were conducted using R v 3.6.3 (R Core Team 2020); we ran GLMMs using the lme4 package (Bates et al. 2015) and GEEs using the geepack package (Højsgaard et al. 2005). We report playback treatment effects in the main text, and provide as Supplementary Material details on model structure (Table S1), comprehensive model results (Table S2) and all parameter estimates (Table S3).

RESULTS

We recorded 748 videos in which reactions to the playbacks were quantifiable, over the 182 camera-trap days (24 h periods) of our experiment. We quantified the reactions of 12 species of ungulates (Table 1), capturing the breadth of the ungulate community with the two most common species recorded being impala and warthog, and the others recorded ranging from elephant (1600 kg) and white rhinoceros (1400 kg) to duiker (16 kg) and steenbok (8 kg). We additionally quantified the reactions of three species of large carnivores: spotted hyena, leopard, and lion (Table 1).

Ungulates

Considered as a whole, the ungulate community Ran significantly more often to hearing lions than wild dogs, significantly more to hearing wild dogs than cheetahs, and significantly more to hearing cheetahs than controls, demonstrating a very clear hierarchy of fear (Figure 1A; overall $\chi^2_3 = 72.7$, $P < 0.001$; all pairwise Holm post-hoc tests $P < 0.007$). Impala demonstrated the same clear hierarchy of fear (Figure 1B; overall $\chi^2_3 = 43.2$, $P < 0.001$), with all pairwise comparisons being significant (all $P < 0.02$) except between
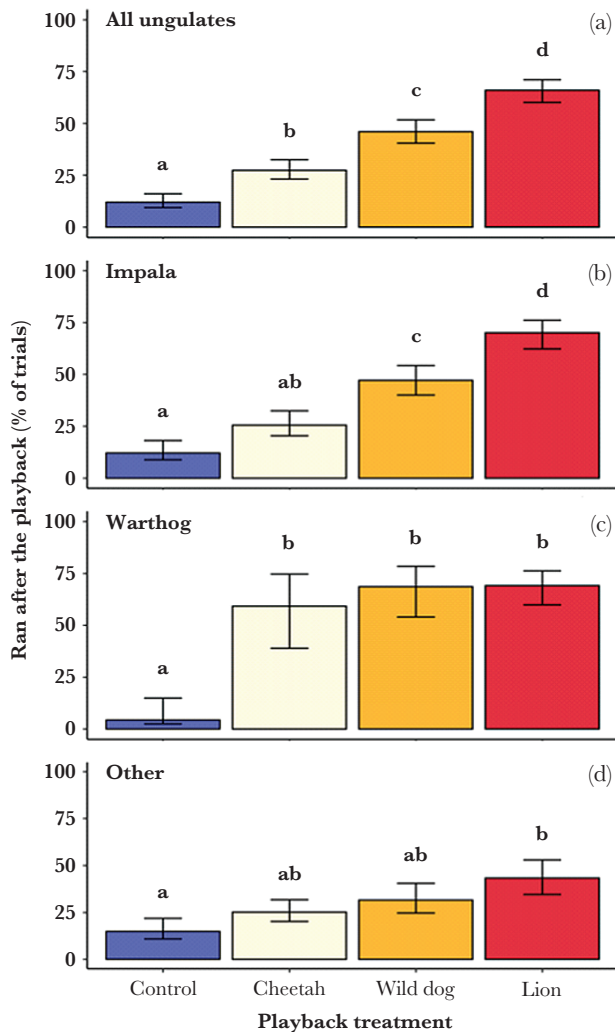
Figure 1

Effects of playback treatment on the probability that ungulates Ran after hearing vocalizations. Predicted percentage of trials in which (A) all ungulates, (B) impala, (C) warthogs and (D) all ungulates other than impala and warthogs Ran in response to control (blue), cheetah (beige), African wild dog (orange), and lion (red) playbacks. Values are marginal effects estimated using generalized linear mixed models (GLMM) with associated standard error bars (mean ± 1 SE). Letters a-d indicate significant differences between treatments ($P < 0.05$ with Holm correction for multiple comparisons).

cheetahs and controls ($P = 0.053$). Warthogs demonstrated a contrasting pattern as they Ran significantly more to all large carnivore vocalizations than to controls but not significantly more to one large carnivore than another (Figure 1C; overall $\chi^2_3 = 13.0$, $P = 0.005$; all pairwise comparisons between large carnivores and controls $P < 0.044$). Importantly, all other ungulates considered as a whole (i.e., excluding impala and warthog) demonstrated the same significant fear of lions as impala (Figure 1D; lions vs. controls, $P = 0.046$), while manifesting respectively lesser responses to wild dogs and cheetah which were not significantly greater than to controls (overall $\chi^2_3 = 7.6$, $P = 0.055$).

Ungulates that did not Run reacted with vigilance on hearing large carnivores, and most so upon hearing lions, as they Looked toward the Sound more to lions (Figure 2; 64% [$N = 31$] of 49

videos) than wild dogs (47% [$N = 40$] of 86), cheetahs (54% [$N = 71$] of 131) or controls (25% [$N = 31$] of 124); there being a significant overall effect of playback treatment ($\chi^2_3 = 30.3$, $P < 0.001$) and significant differences between each large carnivore playback treatment compared with controls (all $P < 0.013$). The same pattern was observed considering impala by themselves (Looked toward Sound; lions, 61%; wild dogs, 50%; cheetahs, 50%, controls, 21%; overall $\chi^2_3 = 19.9$, $P < 0.001$; large carnivores vs. controls, all $P < 0.039$). As for Approaching on hearing a playback, ungulates were only observed to do so on four occasions.

Large carnivores

Whereas ungulates commonly Ran (37% [$N = 230$] of 622 videos), and if not, Looked toward the Sound about half the time (44% [$N = 172$] of 390), and virtually never Approached in response to the playbacks, large carnivores themselves rarely Ran (14% [$N = 14$] of 103), were considerably more likely to Look toward the Sound than ungulates (75% [$N = 39$] of 52), and commonly Approached (40% [$N= 31$] of 78). All of these contrasts between the responses of ungulates and large carnivores were significant (Ran, $\chi^2_1 = 19.6$, $P < 0.001$; Look toward Sound, $\chi^2_1 = 7.6$, $P < 0.006$; Approach, $\chi^2_1 = 50.0$, $P < 0.001$).

Large carnivores were significantly more likely to Look toward the Sound on hearing any large carnivore playback than controls (Figure 3; $\chi^2_1 = 4.66$, $P = 0.039$) but were not significantly more likely to Look toward the Sound on hearing one large carnivore than another (all $P > 0.21$). Large carnivores were about equally likely to Approach on hearing any playback ($\chi^2_1 = 0.07$, $P = 0.796$).

DISCUSSION

Our results experimentally demonstrate that ungulates fear some large carnivores significantly more than others, indicating that the community-level impacts of fear can be expected to differ in systems with multiple large carnivores compared with those where a single large carnivore persists. We demonstrated that ungulates perceived a very clear hierarchy of fear amongst large carnivores, according to which they modulated the intensity of their antipredator reactions. Ungulates considered as a whole reacted more fearfully to hearing lion vocalizations than those of the other two large carnivores, exhibiting a significantly stronger likelihood to Run (Figure 1A), or if that was not the case, to stay and Look toward the Sound (Figure 2), on hearing lions. After lions, ungulates were significantly more likely to Run in reaction to hearing wild dogs than cheetahs. Ungulates that did not run Looked toward the Sound significantly more after hearing large carnivores than controls. Ungulates and large carnivores differed significantly in the ways in which they reacted on hearing large carnivore vocalizations: ungulates Ran or Looked toward the Sound but virtually never Approached, whereas large carnivores themselves seldom Ran, Looked toward the Sound more, and often Approached. Large carnivores, like ungulates, Looked toward the Sound significantly more after hearing large carnivore vocalizations than controls (Figure 3), though they did not look most on hearing lions, as ungulates did (Figure 2).

Ungulates exhibited distinct antipredator reactions to different large carnivore vocalizations, revealing a clear hierarchy of fear amongst lions, wild dogs, and cheetahs. Our multi-predator experimental design demonstrates that these large carnivores are not perceived as equally fearful, and hence are not likely to be functionally interchangeable regarding the fear effects that they exert on the
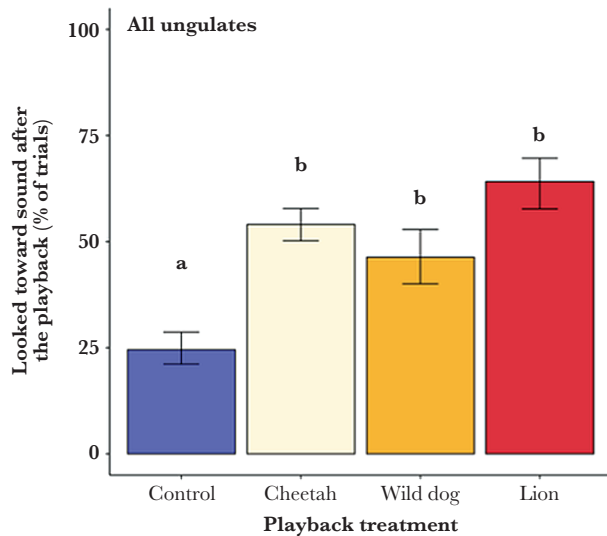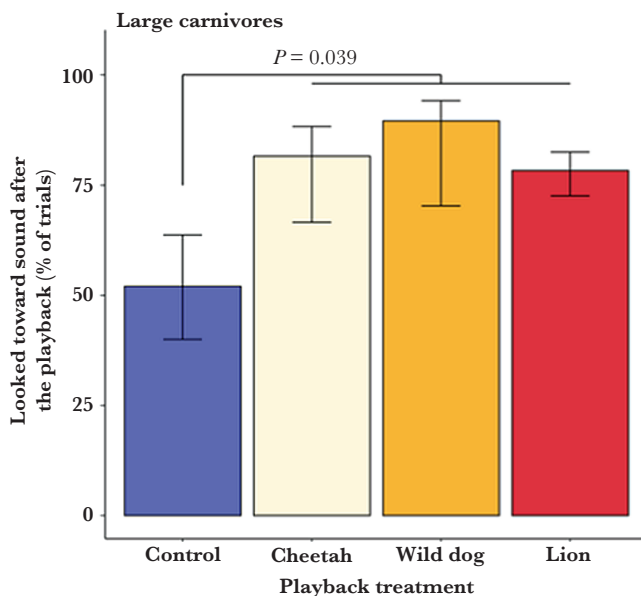
Figure 2

Effects of playback treatment on the probability that ungulates Looked toward the Sound after hearing vocalizations. Predicted percentage of trials in which all ungulates, which did not Run on hearing the playback, Looked toward the Sound in response to control (blue), cheetah (beige) African wild dog (orange), and lion (red) playbacks. Values are marginal effects estimated using generalized estimating equations (GEE) with associated standard error bars (mean ± 1 SE). Letters a and b indicate significant differences between treatments ($P < 0.05$ with Holm correction for multiple comparisons).

Figure 3

Effects of playback treatment on the probability that large carnivores Looked toward the Sound after hearing vocalizations. Predicted percentage of trials in which all large carnivores, which did not Run on hearing the playback, Looked toward the Sound in response to control (blue), cheetah (beige), African wild dog (orange), and lion (red) playbacks. Bars represent marginal effects estimated using generalized estimating equations (GEE) with associated standard error bars (mean ± 1 SE). The P-value shown concerns the contrast between controls versus all predators combined (Wald's $\chi^2_1 = 4.28$).

ungulate community (Schmitz 2007; Weissburg et al. 2014; Griffin et al. 2015; Say-Sallaz et al. 2019). Results from two other new experiments corroborate and extend those from ours. Just as impala

and other ungulates demonstrated a hierarchy of fear to hearing lions, wild dogs, and cheetahs in our experiment, so too did they demonstrate a clear hierarchy of fear to hearing the vocalizations of leopards, spotted hyena, and domestic dogs (*Canis lupus familiaris*), running 50% more often to leopards than hyenas or dogs, in a comparable experiment conducted at a study site roughly 200 km from ours (Epperly et al. 2021). In a complementary experiment testing the reactions of impala to seeing moving, life-size models of lions, wild dogs, and cheetahs, impala were more vigilant on seeing lions and cheetahs than wild dogs (Palmer and Packer 2021), just as ungulates in our experiment were more vigilant on hearing lions and cheetahs than wild dogs (Figure 2). Taken together, the findings from all three new experiments indicate that hierarchies of fear may be the norm in systems with multiple large carnivores, further underlining the importance of factoring large carnivore identity and diversity into our understanding of their community-wide impacts on ecosystems (Schmitz 2007; Say-Sallaz et al. 2019).

The existence of distinct fear reactions to different large carnivore species suggests that recent losses in large carnivore diversity (Ripple et al. 2014; Wolf and Ripple 2017) may bear different consequences on ecosystem functionality depending on which large carnivore species are removed from the system (Heithaus et al. 2008). The experiment by Epperly et al. (2021) provides an illustration. In an earlier study, Ford et al. (2014) thinned vegetation to demonstrate that impalas prefer more open areas and used exclosures to show that this preference mediates the abundance of more or less thorny Acacias. Ford et al. presented correlational evidence suggesting fear of leopards and African wild dogs, which lurk more in woody cover, was the mechanism responsible. Epperly et al. also experimentally thinned vegetation and replicated Ford et al.'s finding that impalas prefer open areas. Epperly et al. combined this experimental thinning with the above described playback experiment and demonstrated that impala and other ungulates fled less on hearing large carnivores in open areas, corroborating Ford et al.'s correlative evidence that fear mediates the preference for open areas, and thus the resulting trophic cascade (Zanette and Clinchy 2020). Critically, the response to leopards in Epperly et al.'s experiment was high in both open and closed areas whereas that to hyenas and domestic dogs was low in open areas and equal to that to leopards in closed areas. Since impala evidently get no respite from their fear of leopards in open areas but do from their fear of hyenas, this suggests the loss of leopards from this system would have less of an impact on this trophic cascade than the loss of hyenas.

In our experiment the ungulate community demonstrated the strongest antipredator reactions to hearing lion vocalizations, in contrast to those of wild dogs and cheetahs (Figures 1A and 2), revealing that ungulates as a whole most feared lions, the system's apex predator (Thaker et al. 2011; Vanak et al. 2013; Creel et al. 2019). This hierarchy of fear with lions at the pinnacle held for impala (Figure 1B) and all other ungulates (Figure 1D), with the curious exception of warthogs (Figure 1C; discussed below). Our multi-predator-prey results experimentally reinforce the inference from prior studies that the fear that lions inspire generally supersedes that of all other large carnivores (Valeix et al. 2009; McComb et al. 2011; Thaker et al. 2011; Favreau et al. 2013; Dalerum and Belton 2015; Creel et al. 2017, 2019; Dröge et al. 2017; Makin et al. 2017). Lions have long been recognized to play a singular role in the functioning of savanna ecosystems as "keystone consumers" (Estes et al. 2011; Ripple et al. 2014; Périquet et al. 2015). To signify the singular fear effects that lions evidently exert on the ungulate community (Figures 1A and 2), we suggest the term "keystone frighteners" be added to their designation as "keystone consumers"

to reflect the entirety of their functional roles in systems with multiple large carnivores.

Our experimental demonstration that the ungulate community as a whole most feared lions is consistent with the third hypothesis presented in the Introduction, that rather than all large carnivores being feared equally or fear varying with species-specific kill rates, fear varies with the likelihood of being killed if the given large carnivore decides to attack (Bouskila and Blumstein 1992; Creel 2018; Palmer and Packer 2021). In our experiment, impala reacted most strongly to lions (Figure 1B), and warthogs reacted to all large carnivores alike (Figure 1C), both patterns being opposite to what would be predicted from published prey preferences for lions, wild dogs, and cheetahs. Data from our study site (Klaserie; de Boer et al. 2010) and a review of 45 studies from across Africa (Clements et al. 2014) show that lions generally avoid preying on impala (Jacob's index [J.I.] < −0.73), whereas wild dogs and cheetahs show positive preferences for impala (J.I. +0.25 and +0.11 respectively; Table 1). Consequently, on this basis, impala would be predicted to react least strongly to lions, contrary to how they actually behaved (Figure 1B). In contrast to impala, warthogs are positively selected for by lions (J.I. > +0.11) although generally being avoided by wild dogs and cheetahs (J.I. −0.52 and −0.41 respectively; Table 1), and warthogs would thus be predicted to react more strongly to lions than either wild dogs or cheetahs, contrary to how they actually behaved (Figure 1C). Similarly, in the aforementioned experiment testing ungulate reactions to models of lions, wild dogs, and cheetahs (Palmer and Packer 2021), predator preference (J.I.) failed to predict fleeing or vigilance by impala, wildebeest (*Connochaetes taurinus*), or zebra (*Equus quagga*).

Rather than predator-specific kill rates, impala and other ungulates (with the exception of warthogs) appear to follow simple "rules of thumb" in determining the safest strategy to survive a predator encounter (Bouskila and Blumstein 1992; Johnson et al. 2013), such as that the greatest danger comes from the largest predator species, or the predator species that attacks in the greatest number (Bouskila and Blumstein 1992; Adams 2003; Benson-Amram et al. 2017; Černý et al. 2019). Why then did warthogs behave differently (Figure 1C)? Adult warthogs generally weigh more than individual wild dogs and cheetahs, warthogs sometimes cooperate in defence, and they can successfully defend themselves against wild dogs and cheetahs, all of which likely explains the negative prey preference for warthogs shown by wild dogs and cheetah (Eaton 1970; Creel and Creel 1995; Clements et al. 2014). The equivalent response of warthogs to lions, wild dogs, and cheetahs thus neither corresponds with these predators' prey preferences nor the apparent danger each would appear to pose in the event of an encounter and is instead consistent with the first hypothesis from the Introduction that large carnivores are interchangeable and all should be feared equally. We suggest warthogs are the exception which proves the rule: the unpredictability of their response well-illustrates why experimental testing remains essential to determine the degree to which different prey fear different large carnivores (see also Palmer and Packer 2021).

One way to view Running, Look toward Sound, and Approaching is as points on a continuum between "flight" and "fight": animals may flee danger, wait and see what the danger is, or move towards it. Our analyses comparing the reactions of ungulates with large carnivores themselves well-illustrates their respective positions on this continuum; with ungulates tending to flee (34% vs. 14%, ungulates vs. large carnivores respectively), whereas large carnivores wait and see (44% vs. 75%) or move toward the danger (1% vs 40%).

The large carnivores whose reactions we recorded included spotted hyenas, lions and leopards (Table 1). We could find no prior experiment documenting the reactions of leopards, but several have tested the reactions of hyenas and lions to playbacks of lions and wild dogs (McComb et al. 1994; Heinsohn and Packer 1995; Watts et al. 2010; Webster et al. 2010). Both ungulates and large carnivores Looked toward the Sound significantly more on hearing large carnivores than controls (Figures 2 and 3), although showing weak or no differences in Looking on hearing one large carnivore versus another. These weak differences may be due in part to the moderate sample sizes but could also reflect Looking toward the Sound being a weaker response to danger than Running, as well as a more ambiguous one. Whereas "flight" (Running) is straightforward, the "wait and see" comprising Look toward Sound may reflect anything from a strong reaction to danger in the form of "freezing", to mere curiosity. A less ambiguous means of titrating fear is to quantify reductions in foraging, as done in studies on many different taxa (Brown and Kotler 2004; Creel et al. 2019), including ABR experiments on ungulates and carnivores (Smith et al. 2017; Suraci et al. 2019b; Crawford et al. 2022; Widén et al. 2022), but this requires a food source, which it was not feasible to provide in our experiment.

The recent manipulative experiments that have begun demonstrating that the fear large carnivores inspire in ungulates can cause trophic cascades have all been conducted on African ungulates, and have addressed the impacts of one or more of lions, wild dogs, cheetahs, leopards, or hyenas (Ford et al. 2014, leopards, wild dogs; Riginos 2015, lions, cheetahs, hyenas, leopards; le Roux et al. 2018, lions, wild dogs; Atkins et al. 2019, leopards). All of these experiments have focused on the aggregate impact caused by the fear of large carnivores considered as a whole. Ours and the two other new related experiments revealing hierarchies of fear among these large carnivores (Epperly et al. 2021; Palmer and Packer 2021), together with the several recent relevant complimentary correlative studies (Thaker et al. 2011; Creel et al. 2017, 2019; Dröge et al. 2017; Makin et al. 2017; Pays et al. 2020), all indicate that the different large carnivores involved would have different impacts with respect to the nature and degree of the cascading effects the fear of them causes, and the experiment by Epperly et al. (2021) we described strongly reinforces this. Comprehensively experimentally testing whether and how fear of different large carnivores affects the strength of trophic cascades could be accomplished by combining the ungulate exclosures, vegetation thinning, and playbacks of multiple large carnivores described in Ford et al. (2014) and Epperly et al (2021), with varying what proportion of the playbacks are comprised of one large carnivore versus another between sites, as done in a recent experiment in Sweden demonstrating that this affected patch use and crop damage by ungulates (Widén et al. 2022). We thus suggest the stage is now fully set to take the next step in experimentally testing if the hierarchies of fear inspired by multiple large carnivores have corresponding hierarchical community-level impacts (Weissburg et al. 2014; Zanette and Clinchy 2020).

SUPPLEMENTARY MATERIAL

Supplementary material can be found at *Behavioral Ecology* online.

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