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BEHAVIORAL ECOLOGY –ORIGINAL RESEARCH

Prey tells, large herbivores fear the human 'super predator'

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Abstract
Fear of the human 'super predator' has been demonstrated to so alter the feeding behavior of large carnivores as to cause trophic cascades. It has yet to be experimentally tested if fear of humans has comparably large effects on the feeding behavior of large herbivores. We conducted a predator playback experiment exposing white-tailed deer to the vocalizations of humans, extant or locally extirpated non-human predators (coyotes, cougars, dogs, wolves), or non-predator controls (birds), at supplemental food patches to measure the relative impacts on deer feeding behavior. Deer were more than twice as likely to flee upon hearing humans than other predators, and hearing humans was matched only by hearing wolves in reducing overall feeding time gaged by visits to the food patch in the following hour. Combined with previous, site-specific research linking deer fecundity to predator abundance, this study reveals that fear of humans has the potential to induce a larger effect on ungulate reproduction than has ever been reported. By demonstrating that deer most fear the human 'super predator', our results point to the fear humans induce in large ungulates having population- and community-level impacts comparable to those caused by the fear humans induce in large carnivores.

Keywords Ecology of fear · Behavioral response · *Odocoileus virginianus* · Perceived predation risk · Playback experiment

Introduction

Humans kill large and medium-sized carnivores at rates far exceeding those of non-human predators, meriting their label as an ecological 'super predator' (Darimont et al. 2015). Recent experiments have demonstrated that the unique and disproportionate predatory pressures humans exact on carnivores are reflected in carnivores fearing humans more than other carnivores (Clinchy et al. 2016; Suraci et al. 2019b), and correspondingly that human-induced fear (antipredator responses) can cause cascading effects across trophic levels at a landscape scale (Smith et al. 2017; Suraci et al. 2019a; Zanette and Clinchy 2020). Fear effects on large herbivore foraging behavior affecting community dynamics have similarly been experimentally demonstrated to result from the fear large carnivores induce in large ungulates (Zanette and Clinchy 2020), and accumulating evidence indicates that foraging costs associated with antipredator behaviors may reduce reproductive rates in large ungulates (Say-Sallaz et al. 2019; Zanette and Clinchy 2020). A recent global meta-analysis of mortality in terrestrial vertebrates suggests that humans not only kill carnivores, but large ungulates as well, at greater rates than non-human predators do (Hill et al. 2019). Thus, large herbivores may be expected to fear humans more than they fear non-human predators (i.e., carnivores), in the same way that carnivores have been shown to fear humans more than they fear other carnivores. Correspondingly, the magnitude of population- and community-level effects caused by the fear humans induce in large herbivores may be anticipated to exceed the demonstrated magnitude of such effects caused by the fear large herbivores have of large carnivores. To explore these potential population- and community-level impacts, it is first necessary to

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test the relative impacts that fear of humans and non-human predators have on large herbivore foraging behavior (Clinchy et al. 2016; Smith et al. 2017; Suraci et al. 2019a, b).

Recent research on white-tailed deer (*Odocoileus virginianus*) conducted in southwestern Georgia, USA, demonstrated that experimentally removing coyotes (*Canis latrans*), the sole non-human predator of adult deer in the system studied, caused deer to be less fearful, spending less time vigilant and more time feeding (Cherry et al. 2015). Correlative evidence in this same system showed that deer fecundity was significantly greater in years when coyote numbers were low (Cherry et al. 2016a), and the experimentally demonstrated effect fear of coyotes has on deer feeding time provides a straightforward explanation for the greater deer fecundity in low coyote years. Other recent studies provide compelling evidence that fear of wolves (*Canis lupus*) affects reproduction in elk (Christianson and Creel 2014), and the fear of cougars (*Puma concolor*) affects reproduction in mountain goats (Dulude-de Broin et al. 2020) and bighorn sheep (Bourbeau-Lemieux et al. 2011). Deer, elk, and bighorn sheep are all hunted in North America, and data from Darimont et al. (2015) indicate that these species are killed by humans at a significantly greater rate than they are by large carnivores (Supplementary online material) and can all thus be expected to fear humans more than they fear large carnivores.

Prior research in our study area experimentally demonstrated that fear of coyotes affects deer feeding time (Cherry et al. 2015) and later linked long-term fluctuations in coyote abundance to deer fecundity (Cherry et al. 2016a, b). Given these site-specific findings, we experimentally tested if fear of humans has an even greater effect on deer feeding time in this system, which would infer a greater effect on deer fecundity. As recent colonizers of eastern North America, coyotes partially fill niches vacated by extirpated large carnivore species, namely wolves and cougars, and often function as the dominant non-human predator of deer in the absence of larger predator species (Cherry et al. 2016b). While coyotes can and do successfully prey on adult deer (Chitwood et al. 2014), human predation rates of adult deer likely exceed those of coyotes in southwestern Georgia (Cherry et al. 2016b) or eastern North America. Data suggest that, even if wolf and cougar populations did persist throughout their historical ranges, humans would remain the leading predator of deer in the system (Darimont et al. 2015). Domestic dogs (*Canis lupus familiaris*) are the other large carnivore extant in this system, but these are not used locally to hunt deer, though feral dogs may kill some deer (Vanak and Gompper 2009).

To test the relative effects fear of humans and fear of coyotes and large carnivores have on deer feeding behavior, we experimentally exposed free-living wild deer to auditory playbacks of the vocalizations of humans, coyotes, wolves, cougars, dogs and non-threatening controls (birds) at baited food patches, and recorded the behavioral responses elicited by each playback. Our experiment followed well-established protocols comparable to those used in demonstrating the fear humans induce in carnivores (Clinchy et al. 2016; Smith et al. 2017; Suraci et al. 2019a, b) including the quantification of three metrics pertaining to foraging behavior: (i) abandonment of the food patch (fleeing) upon hearing a treatment; (ii) reduced time spent feeding upon hearing a treatment among those deer that did not abandon the food patch; and (iii) the aggregate effect hearing a treatment had on the number of times deer were recorded at the food patch in the hour after first hearing the treatment. Combined with our previous work indicating that fear of large carnivores affects deer reproduction (Cherry et al. 2015, 2016a), our results provide strong support for fear of humans having greater population-level impacts on large herbivores. Moreover, the close correspondence between our results and those demonstrating the fear carnivores have of humans (Clinchy et al. 2016; Suraci et al. 2019b) suggests the fear humans induce in large herbivores may have comparable community-level impacts (Smith et al. 2017; Suraci et al. 2019a). We discuss these implications of our results considering recent meta-analyses of worldwide data pointing to fear of humans having pervasive effects on the behavior of mammals of every size and type (Gaynor et al. 2018; Tucker et al. 2018).

Methods

We conducted our experiment at the Jones Center at Ichauway, a 12,000-ha ecological research site located in the lower coastal plain of southwestern Georgia, USA [described further in Cherry et al. (2015, 2016a)], during May–Jun 2018. White-tailed deer are the dominant large herbivore and only native ungulate on-site. Approximately 30% of the estimated population is harvested by humans annually. To measure feeding behavior and to ensure that deer would feed in front of our experimental playback sites, we provided shelled corn at each of 23 sites. We selected playback sites by generating spatially balanced (separated by > = 1 km) random points along the study site's unpaved road network in areas of the property that were treated with prescribed fire during Jan–May 2018. At each random point, we identified the tree nearest to 50 m along a bearing perpendicular to the road at that location, and pre-baited the location with ~ 13 L of shelled corn for 3 days prior to initiation of experimental trials. Once we initiated trials, we visited sites daily to replenish the shelled corn, retrieve data, and maintain electronic equipment.

We recorded deer responses to playbacks using Automated Behavioral Response (ABR) systems, consisting of a video-enabled camera trap linked to a playback unit triggered by the camera's activation (Suraci et al. 2017a). We deployed the playback speaker and camera 5 m from the center of the provisioned corn and programmed the ABRs to broadcast playbacks 10 s into each 20 s video for a playback duration of 10 s. We tested the effects on deer feeding behavior of hearing either humans, coyotes, wolves, cougars, dogs, or controls (birds). To comprise an optimal, non-threatening control composed of familiar, benign hetero-specific animal vocalizations (Hettena et al. 2014), we used the vocalizations of three locally abundant species of birds, the Carolina Wren (*Thryothorus ludovicianus*), Chuck Will's Widow (*Antrostomus carolinensis*), and Barred Owl (*Strix varia*), broadcast during diel, crepuscular, and nocturnal hours, respectively. We designed avian vocalizations to constitute a single treatment (bird sounds) and treated them as such in our analyses (Zanette et al. 2011; Epperly et al. 2021). We used eight exemplars of each species with human exemplars each consisting of a single individual speaking conversationally (i.e., in a neutral fashion not conveying alarm or threat; following Clinchy et al. 2016; Smith et al. 2017; Suraci et al. 2019a, b). We edited all exemplars for consistency in amplitude and quality using Audacity® (Team 2014) and broadcast the playbacks at a consistent mean sound pressure level of 70 dB at 1 m to ensure responses to our stimuli were unrelated to variability in sound intensity across or within treatments, and that the sound was 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. 2019b; Zanette and Clinchy 2020; Epperly et al. 2021). We balanced and randomized treatments across the diel cycle by programming each ABR at each site, such that the treatment broadcast if triggered changed every 15 min. Further, we organized the sequence of treatments for each ABR at each site to avoid order effects and randomly selected exemplars within each 15 min to avoid pseudo-replication (following Epperly et al. 2021; playback schedules used are provided in Supplementary online material). Because the data collected by each ABR comprise a stand-alone playback experiment (complete with treatment and control playbacks), the use of ABRs at multiple sites represents multiple replicates of the same experiment (Suraci et al. 2017a).

We categorized videos as independent treatment-specific exposures if > 60 min elapsed since the last time a deer heard the same treatment at that site, which is more conservative than the > 30 min elapsed time between samples used in most camera trap studies (Suraci et al. 2017b; Epperly et al. 2021). We quantified three impacts of playback treatments on foraging behavior. Upon a deer first hearing a treatment in an independent exposure video, we recorded (i) whether the deer fled (i.e., abandoned the food patch) upon hearing the playback. Regardless of group size, if any individual fled, the response was deemed a flight response. If the subject(s) did not flee, we determined (ii) whether the time spent feeding during the 10 s playback broadcast was less than during the 10 s prior to the broadcast. Both measures were treated as binary responses, i.e., did the deer run or not, and if it did not, did time spent feeding decrease or not. If group size was > 1, mean time spent feeding before and during the playback were used to determine if time spent feeding decreased. Finally, we quantified (iii) the aggregate effect on feeding by tallying the number of videos in which deer were recorded at the food patch in the hour after first hearing a treatment (Smith et al. 2017). While an animal might flee at any sudden sound, or reduce feeding if it does not flee, it would then be expected to return to the food patch to continue feeding at a rate inversely related to how frightening it perceived the sound to be, i.e., the more frightening the less likely it will return, and if it does or did not flee, the less likely it is to spend time feeding.

We used logistic generalized linear mixed-effects models (GLMM), with playback treatment as a fixed effect and site as a random effect. We evaluated treatment-specific effects in independent exposure videos by estimating the probability of deer (i) fleeing or staying and, if the deer stayed, (ii) decreased foraging post-playback relative to pre-playback broadcast. We used a Poisson GLMM, with playback treatment as a fixed effect and site as a random effect, to estimate treatment-specific effects on (iii) the number of videos in which we detected deer at the food patch in the hour following each independent exposure video. We performed all GLMMs using the "lme4" package (Bates et al. 2015) in Program R v 3.6.3 (R Core Team 2020).

Results

We recorded 822 independent exposure videos across 23 sites, with the number of videos being well balanced among the six treatments (control, $n = 159$; coyote, 128; cougar, 138; dog, 126; wolf, 123; human, 148). Upon hearing humans, deer were almost twice as likely to flee (i.e., abandon the food patch) as upon first hearing any species of large carnivore, the contrast between the reaction to humans vs. any given large carnivore being significant in every case (Fig. 1a; all $p < 0.001$). Deer were also significantly more likely to flee from any large carnivore compared to the control playbacks (all $p < 0.001$). Among the carnivore playbacks, deer were equally likely to run whether the large carnivore was extant (coyote), extinct (cougar, wolf), or a human commensal (dog). Deer that did not flee were more than twice as likely to reduce the time they spent feeding (i) if they heard humans or wolves, compared to hearing control playbacks ($p < 0.001$), whereas they were not significantly more likely to do so if they heard coyotes, cougars, or dogs (Fig. 1b). Hearing humans had the strongest impact on (ii) the number of times deer were recorded at the food

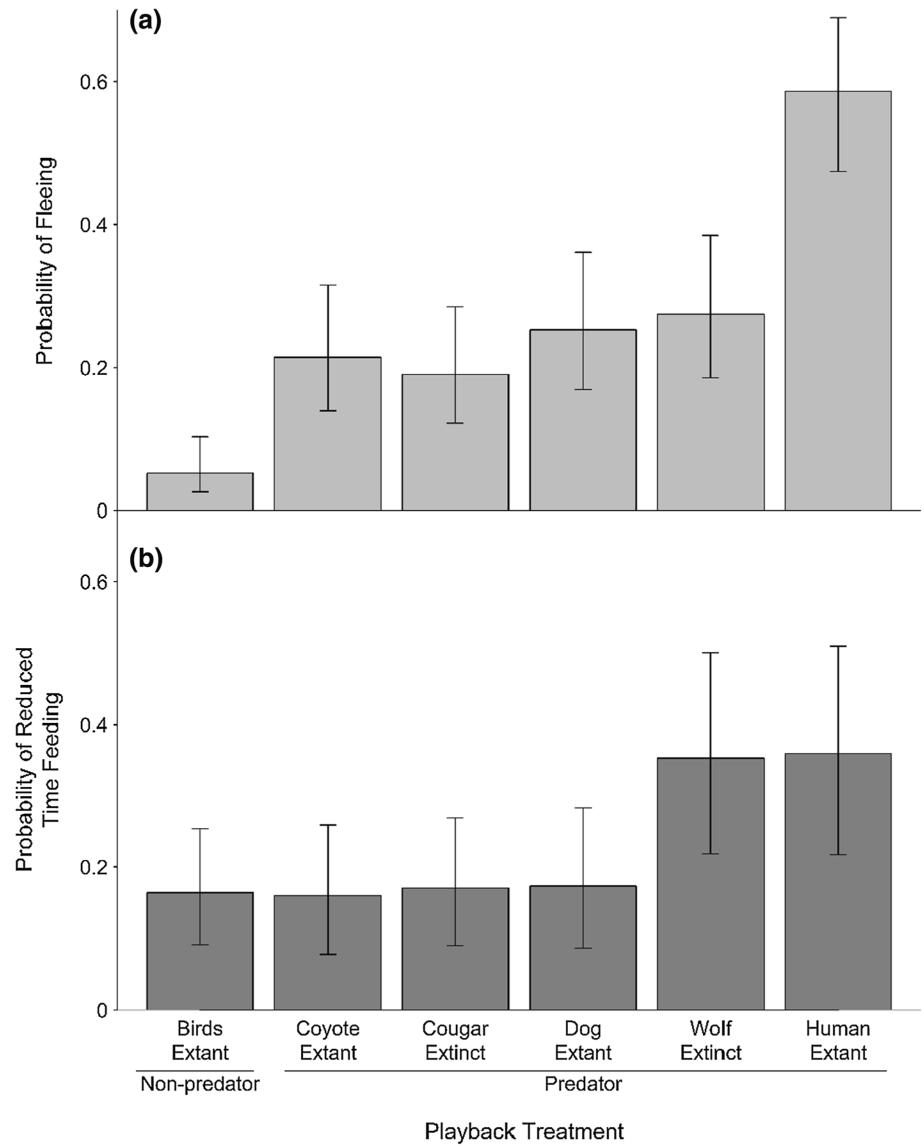

Fig. 1 **a** Predicted probabilities of white-tailed deer fleeing upon first exposure to playback treatments at 23 experimental sites during May–June 2018 at the Jones Center at Ichauway, Newton, Georgia, USA. Control playbacks consisted of extant avian species (Carolina Wren, Chuck Will's Widow, and Barred Owl) while treatment playbacks included extant predators (coyote, dog, and human) as well as locally extinct predators (cougar, wolf). Additionally, we predicted the **b** the probability of reduced time feeding after playback treatments relative to before playbacks initiated for white-tailed deer that did not flee upon first exposure to playback treatments

patch in the following hour (Fig. 2b; see Appendices for additional model results), and hearing any species of large carnivore caused a significant reduction in the number of times deer were recorded at the food patch in the following hour in comparison to hearing control playbacks (Fig. 2a; all $p < 0.001$).

Discussion

Our results experimentally demonstrate that the fear the human' super predator' inspires in large herbivores can exceed their fear of non-human predators, leading to significant relative reductions in time spent feeding, which can be expected to cause fear of humans to have greater population- and community-level consequences than fear of non-human predators. Fear of humans significantly—and most strongly—impacted (i) abandonment of food patches and (ii) time spent feeding if deer did not flee, and consistently had significantly stronger effects on all three metrics than did fear of coyotes, the largest wild carnivore in this system. Hearing coyotes, however, did lead to significant effects on the probability of deer (i) abandoning the food patch (fleeing), and (ii) the aggregate number of times deer were recorded at the food patch, corroborating our previous experimental demonstration that fear of coyotes affects deer feeding behavior (Cherry et al. 2015) and, potentially, fecundity (Cherry et al. 2016a). Human playbacks also had significantly stronger effects on deer feeding than did dog playbacks, suggesting that deer discriminate between humans and their large carnivore commensals (dogs) as demonstrated experimentally in wild carnivores (Clinchy et al. 2016; Suraci et al. 2019b). Interestingly, the non-human predator feared most by white-tailed deer in our

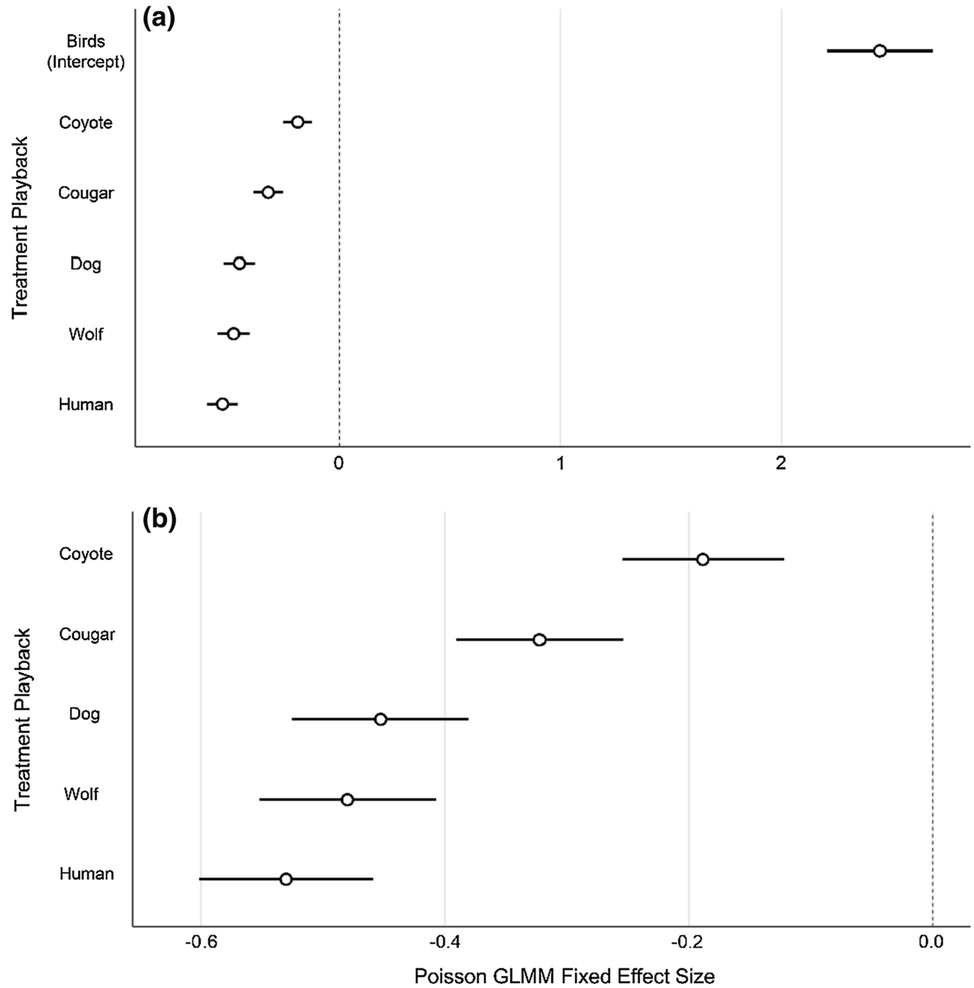

Fig. 2 Model coefficients and their associated 95% confidence intervals estimated with a Poisson generalized linear mixed-effects model of count data representing the number of independent deer detections occurring in the hour following treatment playbacks at 23 randomly selected sites at the Jones Center at Ichauway, Newton, Georgia, USA. **a** Control playbacks consisted of extant avian species (Carolina Wren, Chuck Will's Widow, and Barred Owl). **b** Effects elicited by extant predators (coyote, dog, and human) and locally extinct predators (cougar, wolf) are presented on a magnified scale for ease of comparison. The dashed line indicates zero effect size, and confidence intervals overlapping zero indicate no effect

experiment was not the extant coyote but the extirpated wolf, precisely as demonstrated in a playback experiment on closely related mule deer (*Odocoileus hemionus*; Hettena et al. 2014).

Previous work linking deer fecundity to fear of coyotes (Cherry et al. 2016a) on our study area revealed one of the largest effect sizes reported to date regarding fear of large carnivores affecting large herbivore reproduction (effect size = − 0.47), according to a recent review on the population- and community-level effects of fear in free-living wildlife (Zanette and Clinchy 2020). If fear effects on fecundity are assumed to scale directly with the effects that fear has on feeding (sensu Brown et al. 1999), then given the 27% reduction in (*iii*) the number of times deer were recorded at the food patch caused by fear of humans relative to fear of coyotes (Fig. 2b), the magnitude of the effect on deer fecundity caused by their fear of humans would be projected to be − 0.60; larger than any effect on large herbivore reproduction yet attributed to fear of large carnivores (range = − 0.18 to − 0.55; Zanette and Clinchy 2020). We are of course not proposing that differences in feeding rate translate so directly into differences in fecundity. The actual effect fear of humans has on ungulate fecundity remains to be experimentally tested, and our purpose here is simply to suggest the relative magnitude of effect that might be expected to be found in such an experiment.

Experimental testing, rather than a correlational approach, is essential to determine the magnitude of the effect fear of humans has on deer fecundity given the likely complexity of the effects that humans have on deer. The experiments to date demonstrating that carnivores fear humans more than other carnivores have included species, such as badgers (*Meles meles*), skunks (*Mephitis mephitis*) and opossums (*Didelphis virginiana*), which despite being evidently very fearful of humans nonetheless occur in greater abundance around humans because of the greater availability of food near humans, from agricultural sources or human food waste (Macdonald and Newman 2002; Clinchy et al. 2016; Wang et al. 2015; Suraci et al. 2019a). White-tailed deer abundance in eastern North America has increased dramatically since European settlement because of the increase in food from agricultural sources, greater browse availability due to forest clearing, the extirpation of large carnivores, and other human-caused changes in the environment (Rushing et al. 2020). Our results corroborate the findings from the large number of flight initiation distance studies done on deer and other ungulates in North America (reviewed in Stankowich 2008) by experimentally demonstrating that deer greatly fear humans. Yet the deer in our study still came back for the corn we provided as bait. Fear effects on population and community dynamics are expected precisely because of the trade-off animals must make between time spent on feeding and time spent avoiding predators (Zanette and Clinchy 2020). Humans have a unique ecology in being uniquely dangerous (Darimont et al. 2015), which as our experiment and others demonstrate necessitate animals spending more time avoiding humans, but at the same time, our unique human ecology includes increasing the quantity and quality of food available to many species such that this likely reduces the time they need to spend feeding (Moll et al. 2021). This complexity is why experimentally manipulating one factor at a time (fear in this case) appears the most expeditious means of determining the relative magnitude of the impacts we humans are having on deer and other wildlife.

A growing number of recent experiments have demonstrated that fear of large carnivores can cause trophic cascades by affecting the feeding behavior of large herbivores (Zanette and Clinchy 2020). In our experiment, the high-magnitude fear responses to human playbacks relative to other predators suggests that fear of humans may be more likely to cause trophic cascades than fear of non-human predators. The potential for fear of humans to cause trophic cascades has been experimentally demonstrated in large carnivores (Smith et al. 2017; Suraci et al. 2019a; Zanette and Clinchy 2020). That comparable cascades may be caused by the fear humans inspire in large herbivores is further supported by our results closely corresponding with those from recent playback experiments demonstrating that the feeding behavior of large and medium-sized carnivores is likewise more strongly impacted by hearing the human 'super predator' than hearing carnivores (Clinchy et al. 2016; Suraci et al. 2019b).

In their review of predator playback experiments, Hettena et al. (2014) reported that mammals responded to extirpated felids and canids in 5 of 7 and 6 of 15 experiments, respectively; hence, that extirpated cougars and wolves elicited responses in deer in our experiment was not unexpected. Though prey may respond to extirpated predators, Hettena et al.'s review indicates that preys generally show stronger responses to predators they have been exposed to both currently and historically. In addition to humans, with which deer overlap at both evolutionary and ecological time scales, our comparative experiment included coyotes, a relative newcomer to eastern North America, as well as extirpated wolves and cougars. Our results support the notion that evolutionary and ecological overlap of prey with a predator lends to a heightened ability to recognize and respond to auditory cues for that predator as humans elicited the strongest treatment effect for all three metrics. Interestingly, extirpated wolves (i) reduced the probability of deer foraging following playbacks more and had a stronger (ii) effect on deer feeding behavior than the only extant, wild carnivore in the experiment, coyotes. This finding is in accordance with empirical results reported by Hettena et al. (2014) from their playback experiment targeting mule deer. One potential explanation of the strong effects of wolves relative to coyotes is the evolutionary overlap between deer and wolves; however, it is also of note that coyotes are smaller canids that, in eastern North America, typically hunt singularly or in small packs and more commonly prey on juvenile than adult deer (Benson et al. 2017; Bragina et al 2019). Conversely, wolves are larger and are efficient predators of adult deer (Benson et al. 2017). As such, wolves may be anticipated to elicit stronger responses in deer than their locally novel predator, coyotes. This finding is of particular importance given increasingly common large carnivore restoration efforts intended to preserve or restore ecosystem function via re-establishment of apex predator populations in vacated portions of their ranges (Corlett 2016). One critical concern pertaining to such endeavors relates to the potential inability of naïve prey to respond appropriately upon encountering re-established predators; however, our results suggest that, if wolves were to recolonize or were reintroduced to historic ranges, white-tailed deer populations would be behaviorally responsive to the large canids, likely due to their evolutionary exposure to wolves (Hettena et al. 2014).

Humans have a unique ecology that includes killing large and medium carnivores at rates exceeding those of other, non-human predators (Darimont et al. 2015), and the aforementioned large carnivore restoration efforts are necessitated by human persecution of carnivores large and small (Estes et al. 2011; Di Marco 2014; Ripple et al. 2014). While much research has focused on the effects of human disturbance on wildlife behavior, a growing body of evidence suggests that fear of the human 'super predator' may often be the ultimate driver of wildlife responses to such disturbance. Recent meta-analyses of worldwide data highlight alterations in movement (Tucker et al. 2018) and increases in nocturnality (Gaynor et al. 2018) of terrestrial mammals of all sizes and types in response to human disturbance. These data accentuate that fear of the human 'super predator' appears globally pervasive, and our results suggest potentially pervasive effects on ungulate reproduction as well. Previous experiments have indicated that the fear instilled in large and medium carnivores by the human 'super predator' can affect how frequently large carnivores kill prey (Smith et al. 2017) and induce trophic cascades (Suraci et al. 2019a). Our results elucidate the potential for the fear of humans to cause population- and community-level effects equal to or of greater magnitude than those observed in non-human predator–prey systems and, in concert with previous results from experimental investigations of deer–carnivore interactions in our study area (Cherry et al. 2015, 2016a, b), corroborate recent studies demonstrating the potential for fear of the human 'super predator' to incur far-reaching ecological consequences (Estes et al. 2011; Darimont et al. 2015; Suraci et al. 2016, 2019a; Say-Sallez et al. 2019; Zanette and Clinchy 2020).

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Author contribution statement DAC carried out the data collection and statistical analyses, participated in the design of the study, and drafted the manuscript; LMC participated in the design of the study and critically revised the manuscript; MC participated in the design of the study and helped draft the manuscript; LYZ participated in the design of the study and critically revised the manuscript; MJC participated in the design of the study, helped draft the manuscript, and critically revised the manuscript. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

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Data availability Cleaned datasets and code to reproduce reported results and included figures are available upon reasonable request to the corresponding author and will be made publicly available on Dryad prior to publication.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethics approval Not applicable.

Consent to participate Not applicable.

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