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Running header: **Fear of the human "super predator"**

The fear (perceived predation risk) large carnivores inspire in mesocarnivores can affect ecosystem structure and function, and loss of the "landscape of fear" large carnivores create adds to concerns regarding the worldwide loss of large carnivores. Fear of humans has been proposed to act as a substitute but new research identifies humans as a "super predator" globally far more lethal to mesocarnivores, and thus presumably far more frightening. Although much of the world now consists of human-dominated landscapes there remains relatively little research regarding how behavioral responses to humans affect trophic networks, to the extent that no study has yet experimentally tested the relative fearfulness mesocarnivores demonstrate in reaction to humans versus nonhuman predators. Badgers (*Meles meles*) in Britain are a model mesocarnivore insofar as they no longer need fear native large carnivores (bears, *Ursus arctos*; wolves, *Canis lupus*) and now perhaps fear humans more. We tested the fearfulness badgers demonstrated to audio playbacks of extant (dog) and extinct (bear and wolf) large carnivores, and humans, by assaying the suppression of foraging behavior. Hearing humans affected all of: latency to feed, vigilance, foraging time, number of feeding visits, and number of badgers feeding. Hearing dogs and bears had far lesser effects on latency to feed, and hearing wolves had no effects. Our results indicate fear of humans evidently cannot substitute for the fear large carnivores inspire in mesocarnivores because humans are perceived as far more frightening, which we discuss in light of the recovery of large carnivores in human-dominated landscapes.

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Lay Summary

Large carnivores are frightening beasts but the fear they inspire pales compared to that caused by the human “super predator”. European badgers react somewhat fearfully to the sounds of large carnivores like bears and dogs that can kill them, but are far more frightened by hearing humans. The fear large carnivores inspire can itself shape ecosystems. Fear of humans, being greater, likely has even greater impacts on the environment, particularly in human-dominated landscapes.

Introduction

Large carnivores are frightening beasts and the fear (perceived predation risk) they inspire, particularly in large herbivores and mesocarnivores, has been proposed to play a critical role in affecting ecosystem structure and function (Laundré et al. 2001; Prugh et al. 2009; Ritchie and Johnson 2009; Ripple et al. 2014; Suraci et al. 2016). Recent experimental results confirm that the fear large carnivores inspire in mesocarnivores can indeed have powerful cascading effects down food webs reversing the impacts of mesocarnivores on their prey (Suraci et al. 2016). This recent evidence of community-level effects complements the growing experimental evidence that fear itself can have population-level effects on fecundity and survival in free-living wildlife (Eggers et al. 2006; Zanette et al. 2011; Hua et al. 2014; LaManna and Martin 2016). Loss of the "landscape of fear" (Laundré et al. 2001) the presence of large carnivores creates has accordingly added to conservation concerns regarding the ongoing loss of large carnivores in many parts of the world (Prugh et al. 2009; Estes et al. 2011; Ripple et al. 2014). Where large carnivores are in peril it is often claimed that human hunting could act as a substitute for the role played by nonhuman predators, substituting fear of humans for the fear of large carnivores, but opponents counter that it remains doubtful whether such substitution could actually lead to the same functional consequences for communities and ecosystems (Prugh et al. 2009; Ripple et al. 2014). New research indeed suggests that in much of the world there is no longer any question of fear of humans 'substituting' for the effects the fear of large carnivores has on mesocarnivore behavior, because most mesocarnivores probably already perceive humans as far more frightening, given that humans are in effect a far more lethal "super predator" (Darimont et al. 2015) with a unique ecology entailing disproportionately killing carnivores; illustrated by the fact that averaged across the globe human hunters kill mesocarnivores at 4.3 times the rate they are killed by nonhuman predators (Darimont et al. 2015).

Although much of the world of course now consists of human-dominated landscapes there remains comparatively little research concerning the effects humans have on trophic networks in modified ecosystems (Dorresteijn et al. 2015; Oriol-Cotterill et al. 2015; Smith et al. 2015). Various studies have considered the behavioral reactions of mesocarnivores to human disturbance, including a handful concerning the effects of humans *as* predators (i.e., hunters; Kitchen et al. 2000; Tuyttens et al. 2001; Carter et al. 2007; Monteverde and Piudo 2011; Erb et al. 2012) but none has yet compared the effects of humans versus nonhuman predators. If humans are far more frightening to mesocarnivores than nonhuman predators then the fear of humans may be expected to have even greater effects on ecosystem function. The necessary first step in exploring this is to test the relative fearfulness humans and large carnivores inspire in mesocarnivores in a human-dominated landscape (Dorresteijn et al. 2015; Oriol-Cotterill et al. 2015; Smith et al. 2015).

The "ecology of fear" has been the subject of ever more research since this phrase was coined in the late-1990s (Brown et al. 1999), and numerous experiments have tested the reactions of prey to predator cues of every kind; auditory, visual and olfactory. Audio playbacks provide the most reliable and readily-interpretable means of testing the reactions of free-living wildlife to predator cues (Durant et al. 2000; Eggers et al. 2006; Clinchy et al. 2011; Zanette et al. 2011; Hua et al. 2014; LaManna and Martin 2016; Suraci et al. 2016), and a 2014 review identified 180 such experiments on everything from toads to elephants (Hettena et al. 2014). Several playback experiments have tested mesocarnivore responses to large carnivores (Durant et al. 2000; Watts et al. 2010; Webster et al. 2012; Suraci et al. 2016), but none has tested the reactions of mesocarnivores to humans. Indeed, only two playback experiments to date have tested the reactions of free-living wildlife to humans *as* predators: both African elephants (*Loxodonta africana*, McComb et al. 2014) and pig-tailed langurs (*Simias concolor*, Yorzinski and Ziegler 2007) fled upon simply hearing human voices.

The fate of carnivores in Britain reflects a common progression; the loss of large carnivores (brown bear, *Ursus arctos*, c. 900 AD; wolf, *Canis lupus*, c. 1700 AD; Yalden 1999) was followed by increased human hunting of mesocarnivores (badger, *Meles meles*; fox, *Vulpes vulpes*), both as vermin (bounties offered in Tudor Vermin Act of 1532) and for sport (c. late 1600s, Cassidy 2012). Bears and wolves, where extant, hunt and kill badgers (Seryodkin 2011, Sidorovich et al. 2011), and would have historically done so in Britain. Sport hunting of badgers includes: badger 'baiting', live-trapping a badger and pitting it in fights with dogs; and 'digging', sending dogs into setts (burrows) to corner the badger, then digging it out and killing it (Cassidy 2012). Farmers hunt badgers because they reportedly: dig-up and trample crops; kill poultry and lambs; and interfere with fox hunting (Cassidy 2012). Badger 'baiting' was made illegal in 1835, 'digging' was also in 1973, and badgers and their setts were accorded full legal protection in 1992, but since the 1970s the UK government has sanctioned extensive culling of badgers in aid of controlling bovine TB (Tuyttens et al. 2001; Carter et al. 2007; Cassidy 2012; Macdonald et al. 2015). Badgers thus represent a model mesocarnivore in the sense that they no longer need fear native large carnivores and now presumably have even more to fear from humans.

We experimentally tested the relative fearfulness badgers demonstrate in reaction to playbacks of both extinct (bear and wolf) and extant (dog) large carnivores, and humans. Our results reveal a new dimension to the pervasiveness of humankind's influence on nature (Estes et al. 2011): consistent with humans being far more lethal (Darimont et al. 2015), badgers responded most fearfully to simply hearing human voices. We suggest that rather than acting as a substitute for the fear of large carnivores, fear of humans may commonly have a much greater effect on mesocarnivore behavior than their extinct or extant large carnivore predators, reflecting the human “super predator’s” unique focus on hunting carnivores (Darimont et al. 2015). We discuss the potential effects this may have on mesocarnivore fecundity and survival (Creel and Christianson 2008; Zanette et al. 2011), and their role in mediating trophic cascades (Prugh et al. 2009; Ritchie and Johnson 2009; Ripple et al. 2014; Suraci et al. 2016), particularly in light of the recovery of large carnivores in Europe (Chapron et al. 2014) and proposals to reintroduce large carnivores to human-dominated landscapes such as predominate in Britain (Manning et al. 2009; Svenning et al. 2016).

Methods

Overview of experimental design

Numerous experiments on the “ecology of fear” have titrated fear by measuring facets of foraging at a food patch (Brown et al. 1999; Brown and Kotler 2004; Bedoya-Perez et al. 2013) and this was the approach we adopted. Badgers live in communal burrows termed ‘setts’, spending the day underground and emerging at night to feed (Butler and Roper 1995). We provided badgers with food patches in the form of plastic pails submerged to the rim in their setts that were filled with 150 peanuts mixed in 14 L of sand. We used a repeated-measures design, broadcasting a different playback treatment at each sett on 5 consecutive nights. To control for potential order effects each sett received the treatments in a different order. The 5 treatments were: sheep, dogs, wolves, bears and humans. Sheep were selected as a non-threatening (negative) control, whereas dogs were selected as a positive control that badgers were almost certain to fear (Butler and Roper 2005; Cassidy 2012). Playbacks were programmed to begin broadcasting at sunset, before badgers emerge from their setts, and continued broadcasting until 2 hours after sunset. Sounds were intermixed with silence in a ratio of 1:1.5 (sound to silence) following an established protocol (Zanette et al. 2011; Suraci et al. 2016). Behavior was recorded using motion-activated video cameras that also recorded sound. The behavioral measures of fear that we assayed were: the time of night when badgers first began foraging at the food patch (latency to feed); the time spent vigilant or foraging when they first began feeding at the food patch; and the number of visits to the food patch and number of badgers visiting, over the course of the night (Brown et al. 1999; Brown and Kotler 2004; Bedoya-Perez et al. 2013).

Study site and field procedures

The experiment was conducted in the context of a long-term research project on the ecology of badgers in Wytham Woods (51°46’26”N, 1°19’19”W), Oxfordshire, UK (details see Macdonald et al. 2015), between 6-28 September, 2014; fortuitously during a period of consistently warm, dry weather. Following our repeated-measures design, badger behavior was filmed for 7 consecutive nights (2 nights pre-baiting plus 5 treatment nights) at each of 7 setts.

We positioned two food patches at each sett. Food patches were an average of 1.9 m from a burrow entrance (range 1.3-2.3 m) and 9.0 m apart (range 6.5-11.0 m). A speaker (Ecoextreme, Grace Digital Inc., USA) was positioned adjacent to each patch with the result that each patch was exposed to sound from 2 speakers: the adjacent speaker (5.7 m, range 4.0-9.0 m) and a further speaker (11.8 m, range 6.5-15.8 m) adjacent to the other patch. A motion-activated camera (Moultrie M-990i, Moultrie Products, LLC, USA) was also positioned adjacent to each patch (2.5 m, range 2.2-2.8 m). The camera recorded a 30 s video each time it was triggered. Prior to each night’s filming each food patch was filled with 150 peanuts (shells removed) mixed in 14 L of dry, sifted (1 cm^2 mesh) sand collected from that sett. After each night we searched each patch and never found any remaining peanuts, the badgers having eaten every last one.

Playbacks and behavioral measures

Sound files were acquired from online audio and video databases, and library archives, and then edited and normalized to match peak amplitudes and average duration among treatments (following methods described in Zanette et al. 2011; Suraci et al. 2016) , using Audacity 2.0.3 (http://audacity.sourceforge.net). We used multiple exemplars of each playback type (8 sheep, 11 dog, 10 wolf, 6 bear, 8 human) to compose 2 hour playlists of each treatment. The use of multiple exemplars is standard practice in playback experiments (Kroodsma et al. 2001), enabling robust conclusions concerning responses to the ‘class’ of sounds (e.g., humans speaking) as opposed to the specifics of a particular sound. Exemplars varied in duration (from 10 to 80 s), each was followed by silence 1.5 times the exemplar’s duration (e.g. 10 s exemplar followed by 15 s silence; following Zanette et al. 2011; Suraci et al. 2016), and all were played in random order. Playbacks were broadcast at a volume of 80 dB at 1m, using mp3 players (RCA TH1814WM, VOXX Accessories Corp., USA) plugged into the speakers described above.

To unambiguously titrate the effects of fear we only measured behaviors recorded at the first food patch visited each night. Delaying feeding at the first patch, for example, is readily attributable to fear, whereas when feeding begins at the second is potentially an ambiguous mix of fear and satiation, the badger having already probably eaten all 150 peanuts in the first patch. To quantify the effects of fear on vigilance and foraging, once feeding began, we scored these behaviors in the first 5 videos (150 s) recorded, in which there was just one badger on camera. This excluded any videos (2 of 247) in which badgers might be interfering with one another’s foraging. We operationally defined vigilance as being when the badger had its head up with the long axis of its face not being perpendicular to the ground, whereas foraging was defined as when the badger's nose was touching the ground or the long axis of its face was perpendicular to the ground. Badgers engaged in other behaviors, like scent-marking and grooming, but only infrequently, and these occupied only a small proportion of the time during this initial feeding period. Badgers took about 15-20 min. to find and eat all the peanuts in a patch. If a badger ate all the peanuts in the first patch and then the second and then returned to the first patch (within about 15-20 min.) this would constitute a single foraging bout, the second visit to the first patch thus not being truly independent. To ensure that we were quantifying independent visits we consequently operationally defined independent visits as those separated by ≥ 30 min. At a subset of setts (3) the badgers were all fur-clipped (Macdonald et al. 2015) permitting us to quantify the number of individually-identifiable badgers visiting the food patch in a night. Two observers (DR and JPS) reviewed all the videos to derive the operational definitions of the behaviors and a single observer (DR) scored all the behaviors.

Statistical analyses

We used repeated-measures ANOVAs to test the effects of the playbacks on our five behavioral measures of fear: time of night when feeding began, time spent vigilant, time spent foraging, visits per night, and number of badgers visiting. To verify that our control sound (sheep) was non-threatening we conducted preliminary analyses comparing nights with silence (2 pre-baiting) versus nights with sheep playbacks. Hearing a sound (sheep) caused badgers to attend to it (time spent vigilant: silence, 6.3 s ± 1.6; sheep, 17.4 s ± 1.6; Mean ± S.E.; $F_{1,6} = 10.4$, $P = 0.018$) but otherwise had no significant effect on any of the four measures of foraging (all $P > 0.17$). We thus deemed that our control was non-threatening and conducted all further analyses comparing among our five playbacks, followed by Dunnett's tests (Dunnett 1964) of the significance of each treatment compared to the control (sheep). Prior to analysis all data were Box–Cox transformed (Krebs 1999) and tested for normality and homogeneity of variances. All descriptive results reported (Means ± S.E.) were back-transformed to the original units to aid meaningful interpretation. The descriptive results reported are strictly illustrative reflecting effects among setts rather than within setts.

Results

The power of our results derives from the repeated-measures design of our experiment, which generated a large amount of data. We recorded a total of 2,640 videos over the 49 sett-nights that the experiment extended.

Playback treatment significantly affected the time of night when badgers first began foraging at the food patch (Fig. 1; $F_{4,24} = 7.7$, $P < 0.001$). Hearing the sound of human voices caused the greatest delay in the initiation of foraging, with badgers at 4 of 7 setts waiting until the human playbacks were off before beginning foraging; whereas badgers began foraging prior to the end of every other playback treatment, while sounds were still being broadcast. There was accordingly a highly significant difference between when badgers began foraging on nights with human playbacks, compared to nights with control (sheep) playbacks (Dunnett's test, $P = 0.001$). As anticipated, hearing the sounds of dogs, an extant large carnivore predator, significantly delayed foraging (compared to sheep; Dunnett's test, $P = 0.041$), but surprisingly, so too did hearing the sounds of bears (compared to sheep; Dunnett's test, $P = 0.016$), a long extinct large carnivore. Almost as surprising, given that dogs are domesticated wolves (Yalden 1999) and dog and wolf vocalizations are consequently similar, hearing the sounds of wolves did not significantly delay the initiation of foraging (compared to sheep; Dunnett's test, $P = 0.88$), consistent with badgers having lost their fear of this long extinct large carnivore predator.

Hearing human voices caused badgers to be more vigilant and correspondingly spend less time foraging (Fig. 2). As evaluated in relation to the first 150 s of filming following the initiation of foraging at the food patch, there was no overall treatment effect on the time spent vigilant ($F_{4,24} = 0.6$, $P = 0.68$) nor any significant differences in vigilance between the treatments and control (all $P > 0.86$), and neither was there any overall treatment effect on the time spent foraging ($F_{4,24} = 0.2$, $P = 0.91$) or any significant differences in foraging between the treatments and control (all $P > 0.83$). Because the badgers at every sett initiated foraging while the dog, bear and wolf playbacks were still being broadcast, these results indicate that once badgers had initiated feeding, their subsequent vigilance and foraging behavior was unaffected by the fact that they were still hearing dog, bear or wolf sounds. The same was not true regarding hearing human voices. Some badgers only began feeding after the human playbacks had ended, when there was only silence (4 of 7 setts), whereas others began feeding while the human playbacks were still on (3 of 7 setts). Considering just those setts where badgers initiated feeding while the human playbacks were still broadcasting, hearing human voices did significantly increase the time badgers spent vigilant (Fig. 2a; $F_{1,2} = 24.5$, $P = 0.038$) and correspondingly significantly decreased the total time badgers spent foraging (Fig. 2b; $F_{1,2} = 21.2$, $P = 0.044$).

Hearing human voices reduced the number of visits to the food patch in a night and the number of badgers visiting (Fig. 3). Playback treatment significantly affected the number of visits per night to the food patch (separated by ≥ 30 min.; $F_{4,24} = 2.9$, $P = 0.044$) and the number of individually-identifiable badgers visiting per night ($F_{4,8} = 6.5$, $P = 0.012$). Both these overall treatment effects resulted largely from the response to hearing human voices. On nights when human voices were broadcast there were significantly fewer visits to the food patch (Fig. 3a; Dunnett's test, $P = 0.016$) and significantly fewer individually-identifiable badgers visited

(Fig. 3b; Dunnett's test, $P = 0.008$), whereas no other treatment differed significantly from the control (sheep; all $P > 0.10$).

Discussion

Hearing humans speaking significantly affected every measure of fear. Hearing humans delayed the initiation of foraging (Fig. 1), increased vigilance and decreased the time spent foraging (Fig. 2), and reduced the number of visits and number of badgers visiting the food patch (Fig. 3). The response to hearing human voices was quantitatively and qualitatively different from that to hearing dogs and bears. Whereas hearing dogs and bears did delay foraging (Fig. 1), the delay caused by hearing human voices was respectively 228 % and 189 % greater. Moreover, whereas the badgers at every sett began foraging while the dog and bear sounds were still being broadcast, at most setts the badgers were deterred from initiating foraging until after the human playbacks were off. In addition, hearing dogs or bears had no significant effect on vigilance or the time spent foraging, or the number of visits or number of badgers visiting the food patch, in contrast to the significant effects hearing human voices had on all of these behaviors (Figs. 2 and 3). Taken together, our results demonstrate that badgers were substantially more fearful of humans than their extant or extinct large carnivore predators, consistent with the human "super predator" being far more lethal (Darimont et al. 2015)

Experiments on diverse species, including free-living wildlife (Eggers et al. 2006; Zanette et al. 2011; Hua et al. 2014; LaManna and Martin 2016), have demonstrated that the effects of fear on prey demography may be as great, or greater, than the effects of direct killing by predators (Preisser et al. 2005; Creel and Christianson 2008). The demographic effects of fear need not increase in direct proportion to direct killing (Creel and Christianson 2008; Creel 2011), but recent theory suggests this is likely, if fear affects foraging (MacLeod et al. 2014).

Our results point to a positive association between the relative fear of humans and their relative lethality, and the fact that what we demonstrated were effects on foraging thus suggests the fear of humans likely has demographic effects proportional to direct killing by humans (MacLeod et al. 2014). The total impact humans have on the demography of mesocarnivores could thus be twice that indicated by the level of direct killing. That the fear of humans affected foraging also means that this definitely may be expected to mediate the role of mesocarnivores in causing trophic cascades (Prugh et al. 2009; Ritchie and Johnson 2009; Ripple et al. 2014; Suraci et al. 2016). The new research identifying humans as a "super predator" reveals that the numerical suppression of mesocarnivores by humans far exceeds that of large carnivores (Darimont et al. 2015), and our results indicate that the concomitant fear of humans likely also has effects on mesocarnivore demography and behavior that correspondingly far exceed those caused by the fear of large carnivores. As noted in the *Introduction*, the fear large carnivores inspire in mesocarnivores can have powerful cascading effects affecting ecosystem structure and function (Prugh et al. 2009; Ritchie and Johnson 2009; Ripple et al. 2014), as has recently been experimentally verified (Suraci et al. 2016). Our research documenting how much more fearful mesocarnivores may be of humans provides the necessary first piece of the puzzle in determining if the fear of humans has even more powerful effects on trophic networks in modified ecosystems (Dorresteijn et al. 2015; Oriol-Cotterill et al. 2015; Smith et al. 2015).

The costs and benefits of fear govern predator recognition (Blumstein and Daniel 2005; Blumstein 2006). Escaping predation is the obvious benefit of accurate predator recognition. At the same time, reacting to predator cues can entail significant fitness costs, as demonstrated by the recent predator playback experiments on free-living wildlife documenting resulting reductions in fecundity and survival (Eggers et al. 2006; Zanette et al. 2011; Hua et al. 2014;

LaManna and Martin 2016). Because these experiments involved no actual predation risk, unresponsive individuals would be selectively favoured and one would expect predator recognition to be lost if these manipulations were continued over one or more generations. Loss of recognition of wolf vocalizations has been demonstrated to occur in large herbivores (bison, *Bison bison*; caribou, *Rangifer tarandus*; elk, *Cervus elaphus*; moose, *Alces alces*) in as little as 50 years (Berger et al. 2001; Berger 2007), and our results indicate that the same may occur in mesocarnivores.

In contrast to their lack of reaction to wolf vocalizations, our results suggest badgers may have retained the ability to recognize bears as a threat even though bears have been extinct in Britain for at least 1,000 years (Yalden 1999). Retention of threat recognition over millennia is intriguing but not unprecedented (Blumstein 2006). As already stated, predator recognition is governed by the costs and benefits of fear. Assuming the cost is the same, retaining fear of bears and losing the fear of wolves suggests the former conveys a greater benefit, possibly because bears are more dangerous (Seryodkin 2011: Sidorovich et al. 2011), or because responding to something that sounds like a bear helps the hearer escape from danger. Auditory predator cues are arguably the most species-specific (Blumstein 2006) suggesting badgers specifically recognized bear vocalizations, though they may have reacted to some more general characteristic of the sound, such as its novelty. The fact badgers did not react to wolves, demonstrates they did not simply react to novel sounds, and were able to discriminate between what are arguably members of the same species, i.e. wolves and dogs (Yalden 1999), indicating they were reacting to specific characteristics. Badgers responded to dogs (Fig. 1), and as a growling dog signals an imminent threat, their response to the sound of growling bears could reflect their reacting to a specific cue (growls) rather than a specific species. Raccoons (*Procyon lotor)* discriminated between these same dog and bear playbacks in a similar experiment (Roberts 2014), responding to dogs but not bears, indicating that at least some mesocarnivores can differentiate these cues, suggesting badgers may as well, and may have specifically reacted to bears as bears.

The retention or loss of predator recognition has received considerable attention in the conservation literature (Blumstein and Daniel 2005; Blumstein 2006; Carthey and Banks 2014; Hollings et al. 2015), and has been demonstrated to be directly pertinent to the restoration of large carnivores (Berger et al. 2001; Berger 2007). Recolonizing bears in Sweden and recolonizing bears and wolves in the U.S. killed more moose along colonizing fronts than where bears, wolves and moose had long cohabited, because where moose had been isolated from their large carnivore predators they had evidently lost their recognition of the danger these predators posed (Berger et al. 2001). In moose, recognition was restored in a single generation (Berger et al. 2001), and the same pattern was evident in other large herbivores (Berger 2007). Our results suggest that having evidently lost their recognition of wolves, badgers may similarly suffer increased predation where wolves are recolonizing (Chapron et al. 2014) or are reintroduced (Manning et al. 2009; Svenning et al. 2016), but may not suffer increased mortality from bears, because they have evidently retained their recognition of the danger bears pose.

Behavioral suppression of mesocarnivores by larger carnivores can have powerful cascading effects down food webs capable of shaping ecosystem structure and function (Prugh et al. 2009; Ritchie and Johnson 2009; Ripple et al. 2014), as recently experimentally demonstrated (Suraci et al. 2016). Our results support those who contend fear of humans is unlikely to serve as a substitute leading to the same functional consequences for communities and ecosystems (Prugh et al. 2009; Ripple et al. 2014), because the behavioral suppression the fear of humans induces is substantially greater, in accord with the human “super predator’s” disproportionate lethality

(Darimont et al. 2015). In human-dominated landscapes, such as in Europe, our data indicate that the recovery (Chapron et al. 2014) or reintroduction (Manning et al. 2009; Svenning et al. 2016) of large carnivores is not likely to 'restore' fear to mesocarnivores 'released' from behavioral suppression (Prugh et al. 2009; Ritchie and Johnson 2009), but will instead add to the elevated fear mesocarnivores are evidently experiencing – living in fear of the human "super predator" in a human-dominated landscape. In such circumstances a fully-effective conservation policy should include integrated actions ameliorating the persecution of large carnivores and mesocarnivores alike (Darimont et al. 2015; Dorresteijn et al. 2015; Oriol-Cotterill et al. 2015; Smith et al. 2015).

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Figure captions

Figure 1. Effects of playbacks on the time of night when badgers began foraging at the first food patch, measured in minutes after sunset. Red bars indicate extant predators; grey bars signify extinct predators; and the blue bar identifies the non-predator control (sheep). The horizontal dashed line indicates 2 hours after sunset, when the playbacks turned off. Asterisks signify significant differences (* $P < 0.05$; *** $P < 0.001$) in Dunnett's tests comparing treatments and the control (sheep). Values are Means ± S.E.

Figure 2. Effects of control (sheep) and human playbacks on (a) the time spent vigilant (s) and (b) the time spent foraging (s) in the first 150 s of filming, once feeding began at the first food patch. Values are Means ± S.E.

Figure 3. Effects of control (sheep) and human playbacks on (a) the number of visits to the food patch (separated by $\geq$ 30 min.) and (b) the number of individually-identifiable badgers visiting, per night. Values are Means ± S.E.

Figure 1

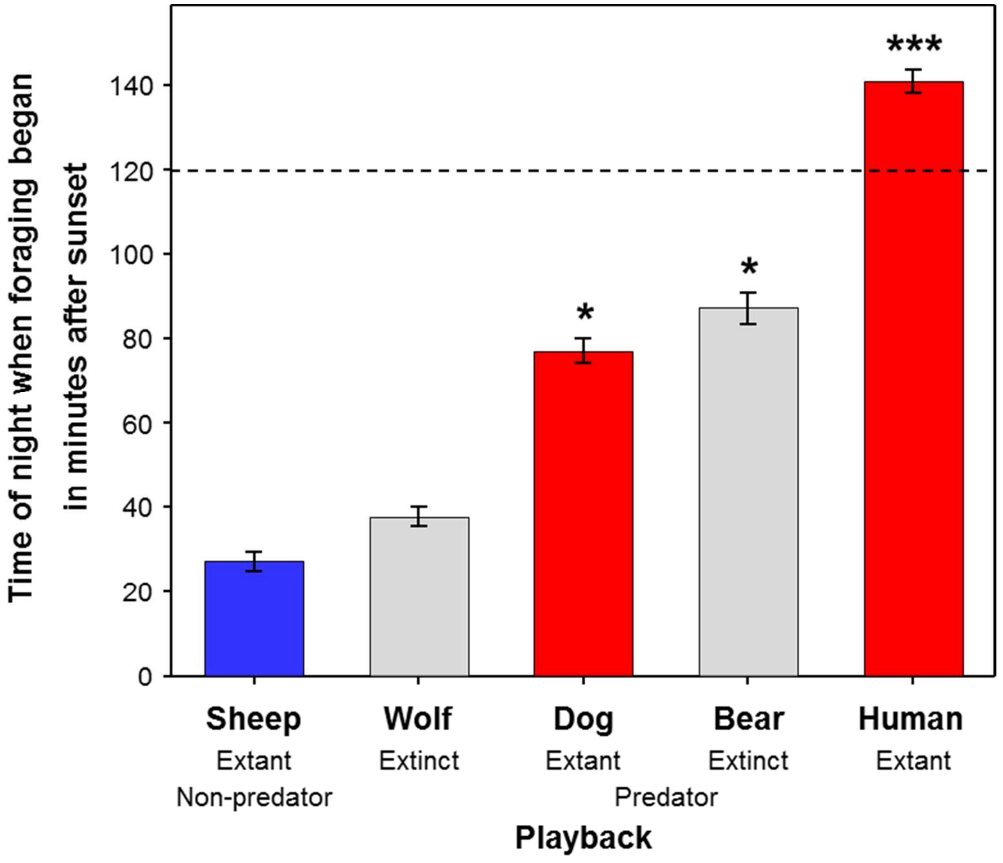

Time of night when foraging began in minutes after sunset
0
20
40
60
80
100
120
140
*
*
***
Sheep
Extant
Non-predator
Wolf
Extinct
Dog
Extant
Bear
Extinct
Human
Extant
Predator
Playback

Figure 2

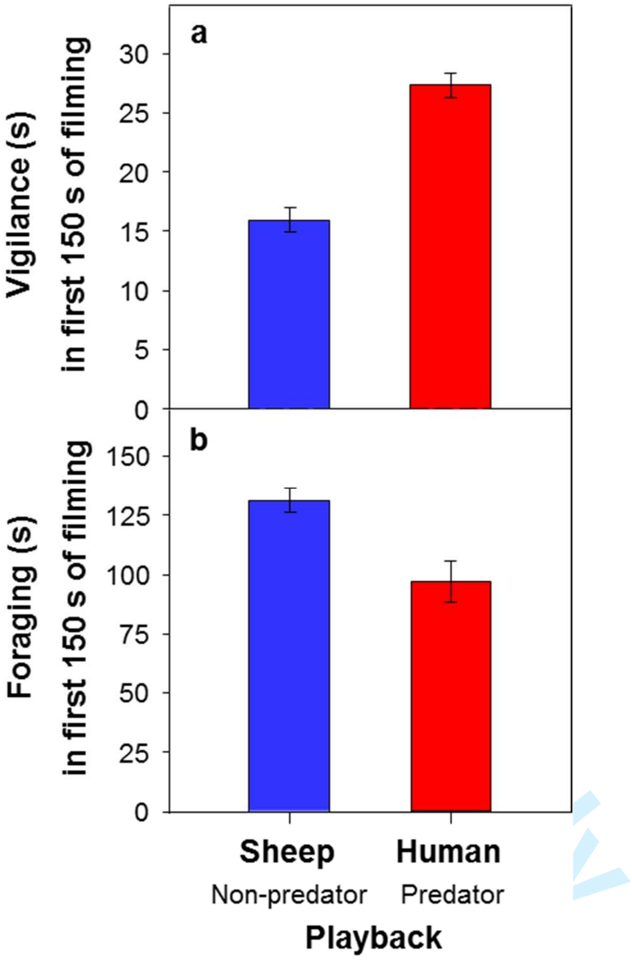
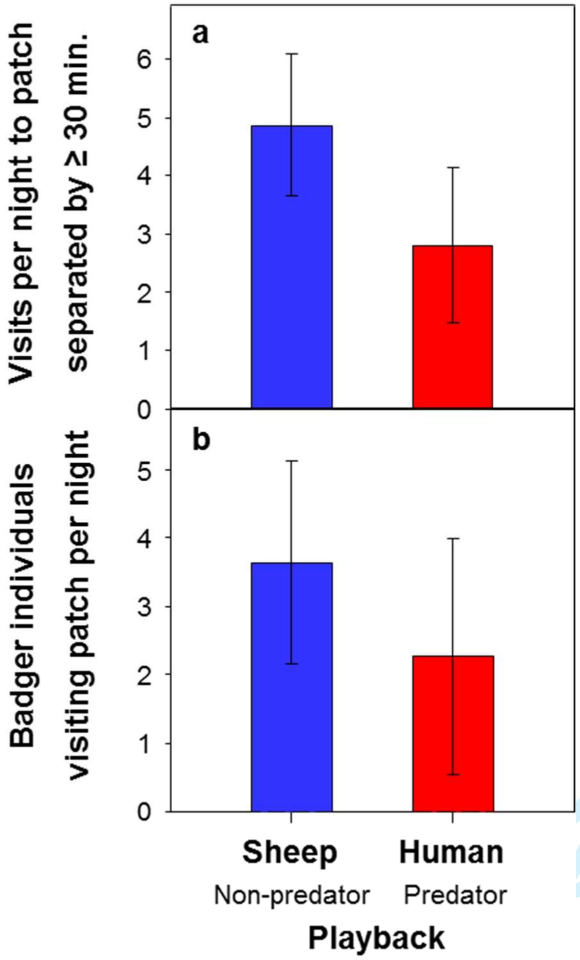

a
Vigilance (s)
in first 150 s of filming
0
5
10
15
20
25
30
b
Foraging (s)
in first 150 s of filming
0
25
50
75
100
125
150
Sheep
Non-predator
Human
Predator
Playback

Figure 3


a
Visits per night to patch separated by ≥ 30 min.
0
1
2
3
4
5
6
b
Badger individuals visiting patch per night
0
1
2
3
4
5
Sheep
Non-predator
Human
Predator
Playback