Current Biology

Report

Wolves and their prey all fear the human "super predator"

Highlights

- Fear in, and of, the "big bad wolf" dominates discourse on human-wildlife conflict
- Fear of humans in wolves and their prey was tested in an unprecedented experiment
- Fear of humans prevails in wolves and their ungulate prey, trapping all in the dark
- Even where legally protected, the big bad wolf fears the human "super predator"

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In brief

Kasper et al. experimentally demonstrate that wolves and their ungulate prey significantly fear humans, thereby verifying that fear of predominantly diurnal humans causes all to be nocturnal. Wolves remained fearful of humans even where legally protected, indicating that accessing human-related foodstuffs—not fearlessness—best explains why wolves ever risk encounters with the human "super predator."

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Report

Wolves and their prey all fear the human "super predator"

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SUMMARY

Fear in, and of, the "big bad wolf" dominates much of the public discourse on human-wildlife conflict and much recent research in large carnivore ecology.[1–9] Global surveys show humans kill prey at much higher rates than other predators,[10–12] and recent experiments have demonstrated corresponding paramount fear of humans and resulting community-level impacts in diverse mammals.[13–24] Humans kill wolves at particularly high rates,[1,3,5,6,10,25] yet fear of humans in wolves and resulting community impacts remain experimentally untested.[1,5,6,8,14,21,26] In the absence of experiments, greater wolf nocturnality where humans are present is invoked as indicating wolves fear humans,[27–29] but alternative interpretations exist. We experimentally tested fear of humans in wolves and their ungulate prey and quantified their nocturnality in a representative human-dominated European landscape[1,28] using automated camera-speakers broadcasting playbacks of humans, dogs, or non-predator controls (birds).[14–20] Wolves and their prey all significantly feared humans. Wolves (n = 101 independent trials) and their prey (n = 225) were more than twice as likely to run (p = 0.004), and twice as fast to abandon the site ($p < 0.001$), in response to humans compared with controls. Wolves and their prey were equivalently nocturnal, and were all significantly more nocturnal than humans ($p < 0.001$). Our results experimentally verify that fear of humans traps wolves and their prey in the dark,[1,29,30] thus corroborating the universality of wolves' fear of humans,[28] and thereby help re-focus the discourse on human-wolf conflict from ostensibly fearless wolves[1,5,6] to human food subsidies better explaining why fearful wolves risk encounters with the human "super predator."[21,31–35]

RESULTS AND DISCUSSION

Fear in, and of, wolves has been a dominant focus of research in large carnivore ecology for over two decades[1,7–9] and shapes much of the discourse concerning human-wildlife conflict.[1–6] Experiments during this time have demonstrated that the fear (antipredator behavioral responses[21]) predators inspire in free-living wildlife can itself reduce prey population growth rates,[36,37] and fear of large carnivores can cause trophic cascades.[38–41] The fear humans inspire in large carnivores, mesocarnivores, and ungulates has in turn been demonstrated to cause cascading impacts on ungulates, rodents, and plants[20–24] in experiments simply broadcasting playbacks of people speaking. Global surveys concerning the "unique ecology of human predators"[10,11] show humans kill large carnivores at more than 9 times the rate they are killed by non-human predators,[10] and humans generally kill medium and large mammalian prey at much higher rates than other predators,[10,12] which, together with the use of "killing technology"[10,11] (e.g., dogs[10]), merits humans being deemed a "super predator."[10,21] Consistent with humanity's unique lethality, multiple recent experiments have demonstrated that fear of the human super predator far exceeds that of other predators in diverse carnivores, ungulates, and marsupials worldwide.[13–20] Despite the long focus on wolves and fear, there remain no experimental tests of the population- or community-level impacts caused by the fear of wolves, nor of whether and to what degree wolves fear humans.[1,5,6,8,14,21,26]

Wolves are among the most heavily hunted large carnivores[10] and were hunted to near extinction in large parts of Europe and the US.[1,3,5,6,25] Legal protection over the past few decades and a

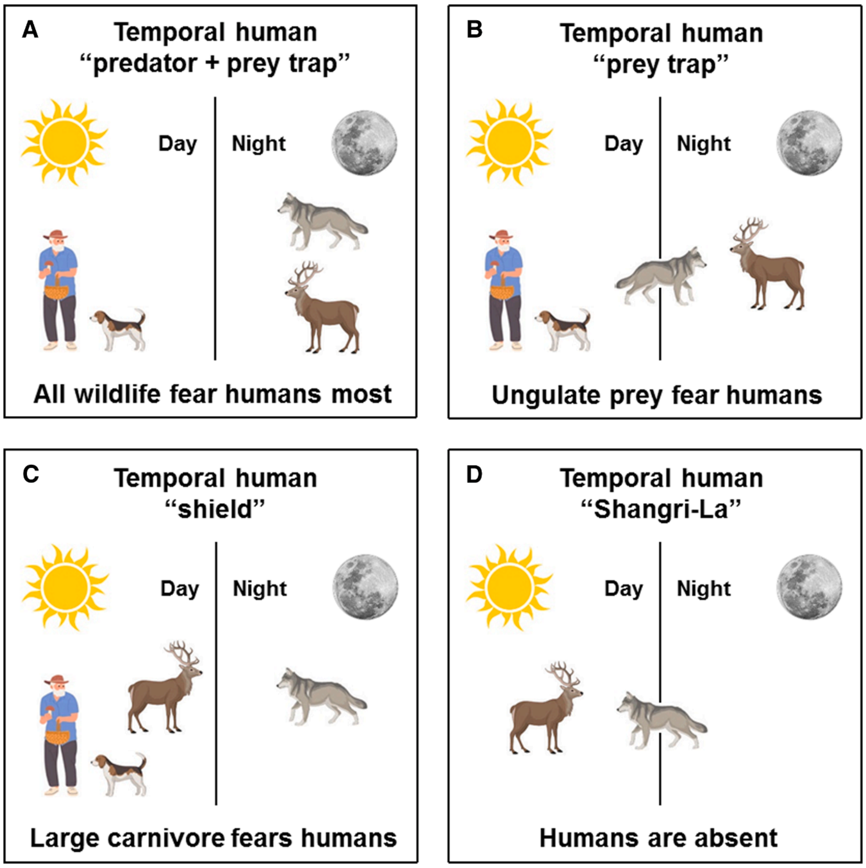

Figure 1. Potential effects of fear of humans or wolves on the diel activity of wolves and their ungulate prey

(A) Paramount fear of humans in both wolves and their ungulate prey causes both to become more nocturnal to avoid primarily diurnal humans, trapping both predator (wolf) and prey in the dark.

(B) Paramount fear of humans traps ungulate prey in the dark, causing wolves to become more nocturnal, not because they fear humans, but because they are tracking their prey's behavior.

(C) Fear of humans traps wolves in the dark, enabling their prey to "shield" themselves by associating with primarily diurnal humans, provided prey fear humans less than wolves, despite humans being demonstrably more lethal.

(D) Where humans are absent, in a wildlife "Shangri-La" because free of humans to fear, fear of wolves causes their prey to become more diurnal, causing wolves to as well, in tracking their prey's behavior.

sufficiency of prey have enabled wolves to reoccupy much of their historical range.[1–3,5,6] This has inevitably led to increased human-wolf encounters, which are often ascribed to wolves having lost their fear of humans.[1,4–6] In the absence of experimental evidence demonstrating that wolves fear humans, the predominantly nocturnal behavior of wolves has been interpreted to suggest they do,[27–29] but this is in no way conclusive. Fear of humans has been experimentally demonstrated to cause wildlife to become more nocturnal,[13,23] and the uniquely lethal danger the human super predator poses to large carnivores and ungulates alike means both wolves and their prey can be expected to become more nocturnal to avoid primarily diurnal humans, trapping both predator and prey in the dark[1,29,30] (Figure 1A). The same pattern, however, could result if wolves do not fear humans but are tracking a nocturnal shift in their prey driven by the prey's fear of humans[27,30] (Figure 1B), as might arise where wolves are protected while large ungulates are hunted.[1] If wolves are nocturnal and their prey diurnal, this could be interpreted as fear of humans trapping wolves in the dark and fear of wolves driving their prey into the light[1,30] (Figure 1C), but this is open to question, because something further is required to explain how the prey fears the far more lethal human super predator less.[9,14,21] Fear of wolves could cause their prey to become more diurnal, and the wolves too in tracking them[30] (Figure 1D), but likely only where humans are absent.[27,28]

We conducted the first controlled manipulative experiment testing whether the "big bad wolf" fears the human super predator, while simultaneously experimentally testing if the prey of wolves also fear humans, and quantifying the nocturnality of wolves and their prey and the diurnality of humans and dogs. We successfully accomplished this using automated camera-speaker systems,[42] which broadcast playbacks of humans (women and men speaking calmly), dogs (barking), or non-predator controls (birds calling), following a well-established protocol[14–20] (see STAR Methods for details). Wildlife worldwide fear humans more than dogs, as demonstrated in multiple comparable experiments,[13–17,19] but wolves are unique in that dogs are domesticated wolves,[43] and we included dogs as a treatment in part to test if how wolves respond to dogs is unique. We recorded the responses of wolves from 10 separate (genetically identified) packs[44] (n = 101 independent trials; median n per pack = 9.5) and four wolf prey species (red deer, n = 41; roe deer, n = 40; fallow deer, n = 121; wild boar, n = 23; total n = 225 independent trials). To quantify fear, we evaluated (1) if animals ran and (2) the time it took them to abandon the site.[14,20] The experiment was conducted in Poland's Tuchola Forest, which is representative of the human-dominated landscapes wolves are reoccupying.[1,28] Wolves were first sighted in the forest in 2005 and first confirmed to be breeding there in 2013, and there are currently an estimated 15 packs.[45] The forest is heavily used for forestry and recreation, including hunting of wild ungulates.[28] Though wolves are legally protected, instances of illegal killing do occur.[25]

Fear of humans prevails in wolves and their ungulate prey

Wolves and their prey all significantly feared the human super predator (Figure 2; Table S1). Wolves ran from humans more than twice (2.4 times) as often as from controls (Figure 2A; p = 0.004; Table S1; Video S1) and were twice (2.1 times) as fast to abandon the site in response to humans as controls (Figure 2B; p < 0.001; Table S1; Video S1). Considering all four ungulate prey species as a whole, ungulates ran from

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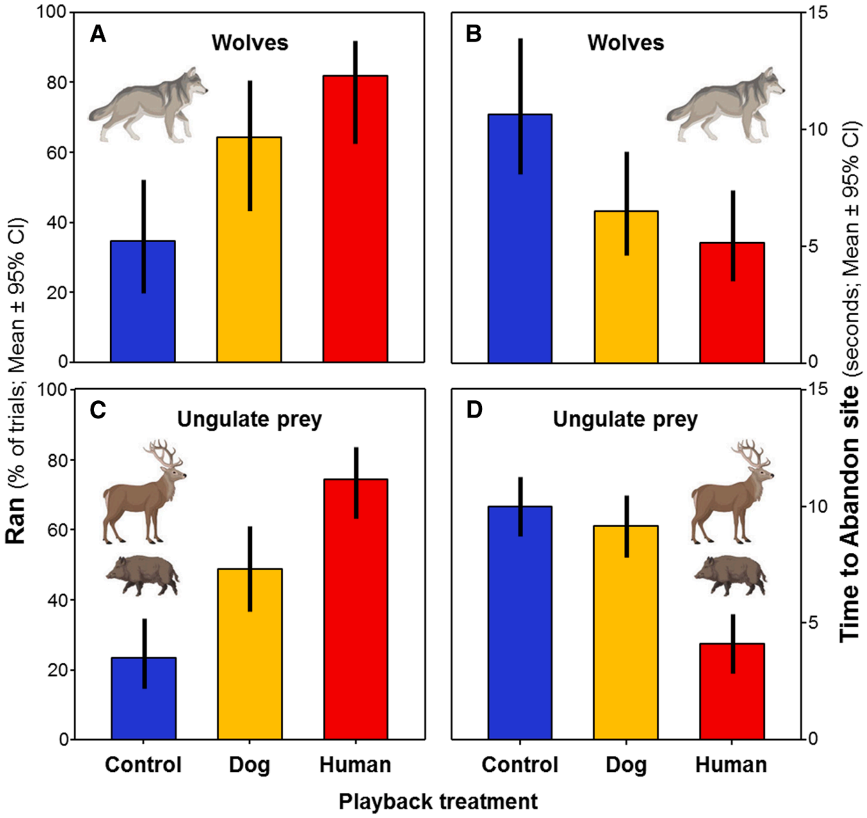

Figure 2. Wolves and their ungulate prey all significantly feared humans

(A–D) Wolves (A) ran significantly more often from humans ($p = 0.004$), and (B) abandoned the site in significantly shorter time to humans ($p < 0.001$), compared with controls; just as their ungulate prey (red deer, roe deer, fallow deer, and wild boar), considered as a whole, also (C) ran significantly more often from humans ($p < 0.001$), and (D) abandoned the site in significantly shorter time to humans ($p < 0.001$), compared with controls. Wolves and their ungulate prey feared humans more than dogs but were not unafraid of dogs, as ungulates (C) ran significantly more often from dogs ($p = 0.005$), and wolves (B) abandoned the site in significantly shorter time to dogs ($p = 0.030$), compared with controls. Illustrated are the mean (± 95% confidence intervals [CI]) percentage of independent trials (see STAR Methods for details; wolf, $n = 101$; ungulate prey, $n = 225$) in which wolves (A) and their ungulate prey (C) ran, and the mean (± 95% CI) time (s) taken to abandon the site by wolves (B) and their ungulate prey (D), in response to hearing control, dog, or human playbacks. Details concerning the recording of responses from the 10 genetically identified wolf packs sampled are shown in Figure S1. Values and details regarding the analyses of each species' responses are reported in Tables S1 and S2. See also Videos S1 and S2.

humans more than three (3.4) times as often as from controls (Figure 2C; $p < 0.001$; Table S1; Video S2) and were more than twice (2.4 times) as fast to abandon the site to humans than controls (Figure 2D; $p < 0.001$; Table S1; Video S2). All four prey species, considered individually, ran significantly more often from humans than controls (all $p < 0.015$; Table S2), and all abandoned the site faster (range = 1.5–3.6 times) to humans than controls, though the latter was only significant in fallow deer ($p < 0.001$; Table S2), the species with the largest sample size ($n = 84$).

Wolves and their prey all feared humans more than dogs (Figure 2; Videos S1 and S2). Both wolves and their prey (ungulates as a whole) demonstrated virtually the same pattern and magnitudes of responses in running more from humans than dogs and more from dogs than controls (Figures 2A and 2C). In the larger sample pertaining to prey ($n = 225$), these treatment differences in running were significant ($p = 0.006$ and $p = 0.005$, respectively; Table S1), whereas in the smaller sample regarding wolves ($n = 101$), they were not ($p = 0.303$ and $p = 0.099$, respectively; Table S1). Wolves and their prey also demonstrated the same pattern in abandoning the site faster to humans than dogs and faster to dogs than controls but differed in the relative magnitudes of their responses to dogs. Whereas wolves abandoned the site significantly faster to dogs than controls (Figure 2B; $p = 0.030$; Table S1), ungulates did not (Figure 2D; $p = 0.497$; Table S1). Individually, all four prey species demonstrated the same pattern of running from and abandoning to dogs as seen among them as a whole (Figures 2C and 2D; Table S2).

Fear of humans traps wolves and their ungulate prey in the dark

Wolves and their prey were all more nocturnally than diurnally active (Figure 3), which in all cases contrasted significantly and dramatically with humans and dogs (all $p < 0.001$; Table S3), which were overwhelmingly diurnal and very rarely nocturnal. Wolves were 4.9 times more nocturnal than humans, and their ungulate prey, considered as a whole, were 4.3 times more nocturnal than humans (Figure 3). Wolves and their prey, as a whole, did not differ significantly in their nocturnality ($p = 0.178$; Table S3), nor did the nocturnality of wolves differ from that of wild boar, red deer, or roe deer, considered individually (all $p > 0.247$; Table S3). Wolves were 1.3 times more nocturnal than fallow deer, which was significant ($p = 0.029$; Table S3), but fallow deer were nonetheless more nocturnally than diurnally active and 3.8 times more nocturnal than humans (Figure 3).

Our results experimentally verify that nocturnality in wolves can be directly attributed to fear of the human super predator trapping both the big bad wolf and its prey in the dark[1,29,30] (Figures 1A, 2, and 3). Our demonstrating this experimentally corroborates the universality of wolves' fear of humans, indicated by recent camera trap results from across Europe,[28] including our own, which show wolves are significantly more nocturnal at multiple sites where humans are present and wolves have reason to fear, as compared with in the Chernobyl Nuclear Exclusion Zone, where humans are effectively absent and wolves thus have nothing to fear (Figure 1D).

Our results also experimentally verify that nocturnality in ungulates (Figure 3) can be directly attributed to the net impact of their

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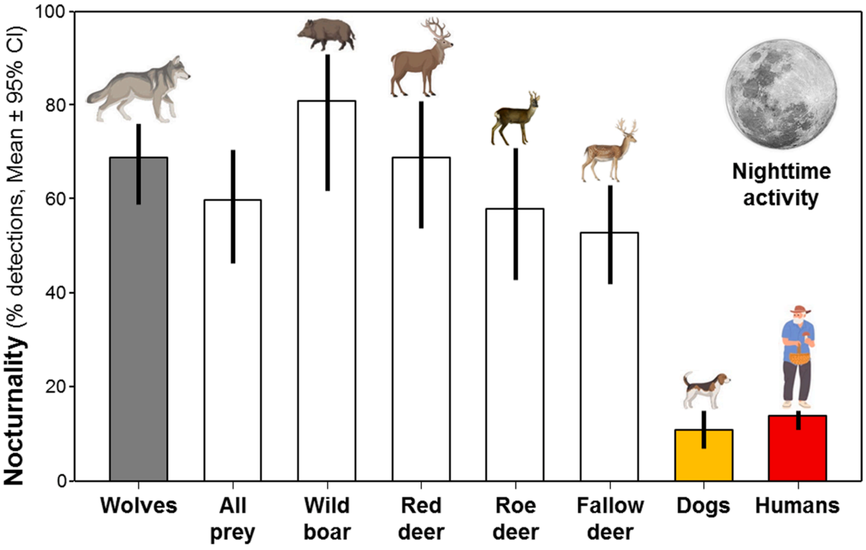

Figure 3. The nocturnality of wolves and their ungulate prey contrasted significantly with that of humans

Wolves and their ungulate prey (wild boar, red deer, roe deer, and fallow deer) were all detected on camera more often at night than during the day, which contrasted significantly with humans and dogs (all $p < 0.001$), which were very rarely detected at night. The nocturnality (% of detections at night) of wolves did not differ significantly from that of all ungulate prey (‘‘all prey’’) as a whole ($p = 0.178$) or wild boar, red deer, or roe deer considered individually (all $p > 0.247$) but was significantly greater than that of fallow deer ($p = 0.029$). Shown are the mean percentage of detections at night (± 95% confidence intervals) concerning wolves (all [night + day] $n = 101$), all ungulate prey ($n = 225$), wild boar ($n = 23$), red deer ($n = 41$), roe deer ($n = 40$), fallow deer ($n = 121$), dogs ($n = 316$), and humans ($n = 4{,}797$). Values and details regarding the analyses of each species’ behavior are reported in Table S3.

simultaneous fear of wolves and humans[30] (Figure 1), when combined with results from a comparable recent experiment on the same species.[20] The comparable experiment demonstrated these ungulates significantly fear humans (as we report; Figures 2C and 2D), significantly fear wolves, and fear humans significantly more than wolves.[20] Being squeezed between their fear of wolves and humans, the relative strength of any temporal shift in these ungulates’ behavior provides a gauge of the relative impacts of these competing fears.[21,30] The lack of any significant difference in nocturnality between wolves and their ungulate prey as a whole, or wild boar, red deer, or roe deer, considered individually, and the contrasting significant and dramatic difference between ungulate nocturnality and human diurnality (Figure 3), strongly corroborates that fear of the human super predator has a far greater impact on these ungulates’ behavior compared with their fear of the big bad wolf. While fallow deer showed a modest reduction in nocturnality attributable to their fear of wolves, they in no sense ‘‘shielded’’ themselves by temporally associating with humans (Figure 1C) but instead maintained a far greater temporal separation from humans than wolves (Figure 3), demonstrating the far greater impact caused by the fear of humans. Critically, the only benefit fallow deer had to gain from temporally shifting their behavior was reduced danger. Most studies purporting to show a human ‘‘shield’’ (Figure 1C) neither consider nor control for the fact that risking associating with humans often comes with benefits such as far greater access to food or other resources.[9,14,21]

Ecological and conservation significance

Paramount fear of the human super predator pervaded the large mammal community we tested in Poland (Figure 2), just as has been experimentally demonstrated in ungulate communities elsewhere in Europe,[20] savanna mammal communities in South Africa,[14] and marsupial communities in Australia,[19] and just as paramount fear of humans has been experimentally demonstrated in individual species of carnivores and ungulates in Europe, North America, and Asia.[13,15–18] Just as we report in wolves (Figures 2A and 2B), leopards, hyenas, and cougars have all been experimentally demonstrated to significantly fear humans and fear humans more than other large carnivores (more than lions, in leopards and hyenas[14]; more than dogs, in cougars[15]). Most prior experiments have tested responses to humans and dogs either because dogs are used in hunting or because they are the only extant large carnivore.[19] Wolves ran from humans 1.3 times more often than dogs (Figure 2A), which is within the range (= 1.3–5.0 times, median = 1.9 times) reported in multiple prior experiments on diverse species regarding the relative fear of humans compared with extant large carnivores.[14,19] In this and all other ways, the fear of humans in wolves, experimentally demonstrated here (Figures 2A and 2B), corresponds in pattern and magnitude with the growing experimental evidence that wildlife worldwide most fear the human super predator.[14,19]

Importantly, the legal protection provided to the wolves in the Tuchola Forest did not cause them to lose their fear of humans. Many of the aforesaid experiments testing wildlife’s fear of humans have been conducted in protected areas or on protected species, like the wolves in Tuchola, and none of these protected animals evince having lost their fear of humans.[13,14,18,19] Even if killing by humans was eliminated, fear of humans could persist just as fear of predators that no longer kill, because they have been extirpated, has been experimentally demonstrated to persist for multiple generations in diverse mammals.[13,16,46,47] But this is immaterial, only possibly being pertinent where humans are effectively absent, as in Chernobyl,[28] because legal protection neither precludes legal killing nor eliminates illegal killing. For example,[48] legal killing, for management, etc., accounted for 27% of wolf mortalities, and illegal killing accounted for at least a further 37%, in four legally protected endangered wolf populations in the US. Numbers in Europe are comparable.[1,25] We refer throughout to the ‘‘big bad wolf’’ because recent reviews report that in the US and Europe, the public’s fear of and animosity toward the big bad wolf far exceeds that of any other large carnivore,[5,6] helping to explain the historical persecution and high rates of illegal killing of wolves and the recent push to remove legal protection from wolves.[1,2,4–6,25] Fear of wolves, moreover, helps explain concerns over wolves ‘‘losing their

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fear" of humans, as this represents a loss of control over wolves and their consequently then being perceived as "problem" wolves.[1,5,6] Experimentally demonstrating that wolves fear humans, as we have done, and fully understanding why they do[1,2,5,6,10,25,48] are thus both critical to moving beyond the question of fearless problem wolves.

Wolf conservation and management can immediately profit from the certainty that the big bad wolf fears the human super predator. By inspiring the greatest fear in wolves, human presence can clearly provide one of the most powerful behavioral deterrents to wolves.[5,14,19,31,49] Simulating human presence using human playbacks is an effective means to exploit this fear of humans, as demonstrated by recent experiments that have deterred cougars,[23] deer,[20] rhinoceroses,[50] and coyotes and elephants (L.Y.Z., unpublished data) from large areas over long periods. The certainty that wolves fear humans is also of great benefit in refocusing attention on what counterbalances this fear, rather than whether wolves are fearless. Fear (anti-predator behavior) is primarily about food: avoiding becoming food while trying to find food.[21] Focusing on this fundamental risk-reward trade-off is critical to identifying where the problem lies. The perception that some animals have lost their fear of humans has been experimentally demonstrated to be attributable to failing to consider the super-abundant, super-quality food humans are normally surrounded by.[32] Our experimental results (Figures 2A and 2B) and those demonstrating the pervasive fear of humans in wildlife worldwide[14,19] strongly indicate that any apparently fearless wolf is more likely a hungry wolf risking proximity to humans to get a bite of our "super food."[21] In this light, the problem is how to keep the wolf from our food—not that there is a fearless problem wolf.[31] Focusing on reducing human food subsidies to wolves and the means to do so is well-discussed in the literature.[31,33–35] What our evidence adds is that there is in effect no alternate problem to contend with—no big bad wolf unafraid of the human super predator.

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Liana Zanette (lzanette@uwo.ca).

Materials availability

This study did not generate new, unique reagents or materials.

Data and code availability

- All data required to replicate the analyses of the results reported in this paper will be shared by the lead contact upon request.
- This paper does not report original code.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

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AUTHOR CONTRIBUTIONS

D.P.J.K., L.Y.Z., M. Clinchy, P.A.S., M. Churski, K.K., E.S.-S., and M.S. designed research. K.K. and E.S.-S. performed research with the support of all other authors. K.K., E.S.-S., N.P., L.Y.Z., and M.Clinchy analyzed data. K.K., D.P.J.K., L.Y.Z., and M. Clinchy wrote the paper with input from all other authors, all of whom approved its publication.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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- EXPERIMENTAL MODEL AND SUBJECT DETAILS
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  - ○ Experimental rationale and design
- METHOD DETAILS
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  - ○ Quantifying nocturnality
- QUANTIFICATION AND STATISTICAL ANALYSIS

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2025.09.018.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Processed video data	Lead contact	lzanette@uwo.ca

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Study area, sites and subjects

The Tuchola Forest is a representative European human-dominated wildlife landscape,[1,28] comprised of pine plantations liberally intermixed with recreational areas, agricultural lands and small towns and villages. The experiment was conducted at 24 sites distributed across an approximately 1,100 km^2 area centered at 53.601° N and 18.188° E (Figure S1). Site selection entailed establishing at least two sites in the active range of each of the 10 identified wolf packs in the area[44,45] (Figure S1). The experiment was performed over 15 weeks, from late summer to late autumn (August-December), during the ungulate hunting season.

We deployed one automated camera-speaker (Automated Behavioural Response; ABR) system[42] per site which operated 24 h/day without any observer present, video-recording the responses of animals to the playback treatments.[14] We evaluated the responses to the treatments in wolves (*Canis lupus*) and four species of their ungulate prey (red deer, *Cervus elaphus*; roe deer, *Capreolus capreolus*; fallow deer, *Dama dama*; wild boar, *Sus scrofa*). The subjects were thus any and all individuals of these five species that triggered an ABR, along with any humans or domestic dogs that did so. Diel activity was quantified from ABR recordings. Any human presence, whether on foot, bicycle or horseback, or in or on a motorized vehicle; was included in our quantification of human diel activity.

We recorded $n = 101$ independent trials of wolf responses to the treatments and $n = 225$ independent trials of their ungulate prey responding to the treatments. We define ‘‘independent trials’’ of responses to the treatments as in prior ABR experiments as comprising recording(s) of a species’ response to a playback treatment separated by > 60 min. since the species last heard that treatment at that site.[14–16,19,20] Human ($n = 4{,}797$) or dog ($n = 316$) detections were similarly defined as independent if separated by > 60 min. Note that this is more conservative than the > 30 min. used to define independence in most camera trap studies.[14–16] Because multiple wolves were recorded in a single video on some occasions (e.g. 3rd and 4th clips in Video S1), the total number of recordings of wolves was $n = 125$. Similarly, because groups of ungulates, particularly boars, were recorded in a single video on some occasions (e.g. 1st clip in Video S2), the total number of recordings of ungulates was $n = 292$. If there were multiple individuals in a video their responses were not considered independent and this was accounted for in the statistical analyses.

This research adhered to Poland’s *Act on the Protection of Animals Used for Scientific or Educational Purposes (2015)* and was approved by the relevant Regional Directorates for Environmental Protection. As this was a camera-trapping experiment on free-living individuals the subjects comprised whatever species, number, age or sex of individual triggered the ABR. Juveniles were rare and because their responses were deemed dependent on their parent’s, only those of adults were evaluated. As wolves were our principal focus, sex was not included in analyses as this was not reliably identifiable in wolves.

Experimental rationale and design

As noted in the Main text, no prior controlled manipulative experiment has tested whether wolves fear humans.[1,8,14,21,26] A recent study reported recording a single video of a wolf hearing a human playback,[26] from which it fled, so there is an anecdote, but no test. The objective of our experiment was to test the relative degree of fear humans inspire in wolves and their ungulate prey. Darwin discussed the lack of ‘‘fear’’ of humans in birds on the Galapagos Islands as evidenced by their not fleeing at the approach of a dangerous predator (himself), so gauging fear on the strength of anti-predator responses is well-precedented.[21] To demonstrate an anti-predator response an animal must perceive a predation risk.[21,36,37] To perceive entails both sensing and understanding. To accordingly rephrase, the objective of the experiment was to quantify the understanding wolves and their prey have of the relative danger humans pose.[21] Ours is not an experiment on sensory ecology, it is an experiment on cognitive ecology.[21] Consequently, the experiment was designed to control for or eliminate crude sensory variation to every degree possible. As detailed below, this was accomplished at three levels: (1) the site; (2) the sound; and (3) the staging. Variation among sites was controlled for by broadcasting all three treatments (humans, dogs, controls) at each site, enabling repeated-measures sampling at each site.[14,16] Variation in crude sound characteristics such as decibel level and rate of onset were controlled for by ensuring these were equivalent across the treatments.[36,37] Finally, within-site variation was controlled for by ‘‘staging’’ where animals were when they heard the playback, e.g. by using the conjunction of roads, or positioning of barriers, to corral them into place.[14,42]

The treatments were designed to comprehensively test the relative fear of humans by including both: (1) a negative, non-predator control (birds), expected to elicit no more than a simple startle (‘‘jump-scare’’) response (e.g. start of 5th clip in Video S2)[46]; and (2) a

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positive, predator control (dogs), expected to elicit the strongest response to a non-human predator.[13–16,19] The positive controls in prior comparable ABR experiments have included apex large carnivores, like lions and leopards[14,18]; whereas dogs have been used as positive controls in other ABR experiments because, like here, dogs are the only extant large carnivore for comparison.[15–17,19,20] As noted in the Main text, using dogs as the positive control in the present experiment provided a possible additional dimension, because wolves are domesticated dogs.[43] Conceivably,[21] wolves could have perceived the danger posed by a congeneric to be greater than that posed by a predator, and the response to dogs could correspondingly have been greater than that to humans.

To accomplish the above noted repeated-measures sampling at each site, all three playback treatments were broadcast at each site by programming the ABR to change which treatment was broadcast if it was triggered, every 15 min. To illustrate, if triggered any time between 00:00 and 00:15 AM one treatment would be broadcast, e.g. dogs, between 00:15 and 00:30 a different one would, e.g. humans, and so on.[14,16,19,20] To ensure the broadcast of treatments was balanced and randomized across the diel cycle each ABR was programmed to broadcast all three treatments in random order, and then do so again in a different random order while avoiding broadcasting the same treatment for > 15 min, and so on, until the whole 24 hr cycle was accounted for.[14,16,19,20] Additional randomization was ensured by programming different ABRs with different sequences. Prior to use we verified that each programmed sequence was free of potential order effects.

A playback was broadcast each time the ABR's camera trap was triggered, beginning 3 s after video-recording commenced and continuing for 10 s. Prior ABR experiments have shown that a 3 s delay is ample to identify a change in behaviour, e.g. a walking animal starts to run demonstrating that it is reacting to the playback.[14,42] A 3 s delay, in combination with careful ''staging'' (described below), also helped ensure the animal was in an optimal position to observe its response (e.g. 4th clip in Video S2).[14,42]

We used 10 exemplars of each playback treatment to ensure responses were to the class of sound (e.g. human vocalizations) rather than the specifics of a particular exemplar.[13] Which exemplar of a treatment was played when the ABR was triggered was randomly selected.[14,16,19,20] Exemplars were chosen which would be familiar to animals in the area, to control for possible variation due to novelty, and accordingly included humans speaking Polish and vocalizations of common local birds.[14,16,19,20] Human exemplars (5 of women, 5 of men) comprised of one individual speaking Polish, calmly in a neutral fashion not conveying alarm or threat, to simulate overhearing people speaking in conversation.[14–20,22] Dog exemplars included common breeds, e.g. Alsatians, Dobermans and hunting hounds.[20] To comprise an optimal, non-predator control composed of benign heterospecific animal vocalizations,[46] we used the vocalizations of Hooded Crows (*Corvus cornix*) and Tawny Owls (*Strix aluco*), broadcast during day and night respectively.[14,16,20] Bird vocalizations were designed to be and treated as a single treatment (controls) in our analyses.[14,16] Sound files were from online archives and personal recordings.

Playbacks were standardized to a volume of 60 dB at 10 m, to simulate the volume of normal human conversation, and be audible but not startling to animals within the 15 m detection range of the camera's motion sensor.[14–16,19] ''Staging'', detailed below, helped ensure animals were generally 10 m distant from the speaker when the playback was broadcast. The onset of each playback was also standardized to ensure the volume was near 60 dB from the start, to prevent confounding the ''Time to Abandon site'', which would occur if the sound increased gradually, because this would introduce variation in when animals first heard the playback.[14,20]

METHOD DETAILS

Field procedures

At each of the 24 ABR sites we created a consistent auditory and visual arena in which to stage the recording of the reactions of animals to the playbacks, following a well-established protocol developed in prior ABR experiments.[14–16,19,22,42] To begin, all of the ABRs were deployed at intersections of forest roads, which helped both channel animals toward the intersection and standardize the physical conditions in which the playbacks were heard and the animals' responses were observed (most clearly illustrated in the 6th clip in Video S1 and 4th and 5th clips in Video S2). At each site we then located a tree 10 m from the intersection and strapped the ABR's camera to the tree at a height of 2.8 m and positioned the connected speaker 0.7 m directly above the camera, helping ensure animals were 10 m distant from the speaker when they heard the playback and thus heard it at a volume of 60 dB. Finally, to help further ensure animals were 10 m distance from the speaker, we corralled them away from the immediate vicinity of the ABR by piling woody debris in a 5 m radius around the tree with the ABR.[14,42]

Quantifying fear responses

We quantified (A) whether animals Ran in response to a playback (yes or no) because running (fleeing) is among the most straightforward behavioural measures of fear[21] and was recognizable in every species.[14] We operationally defined running as taking three or more rapid steps.[14] To qualify as running in response to the playback, the animal had to be visible both before and after the playback began and not already running.[14,16] We quantified (B) ''Time to Abandon site'' by calculating the time (s) elapsed between the start of the playback and the last time the animal was in view, or the video ended.[14,20] Running and time to abandon are complementary measures of fear and are in no way redundant.[14] To illustrate, animals may run rapidly away from the site (e.g. clips 1-4 in Video S1), or they may run, stop, and then more slowly leave the site (e.g. leftmost wolf in 5th clip in Video S1); in both cases the animals have run, and additionally quantifying the time to abandon is essential to differentiate these readily-distinguishable responses. The necessity of quantifying both measures of fear is illustrated in this experiment by the respective significant and non-significant running and time to abandon responses to dogs demonstrated by the ungulates (Figures 2C and 2D). If more than one individual of a species was in view, we quantified the reactions of up to the nearest five individuals, and took their mean (ran, as a binomial;

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rounding up if $\geq$ 0.5) or median (time to abandon) response, as representative of the reaction in that video.[14,20] We ensured high inter-observer reliability by preliminary testing among observers, and following standard experimental procedure, observers were blind to treatment (i.e., videos were muted).[14]

Quantifying nocturnality

Our data on wolf nocturnality are directly comparable to that reported in the recent European survey of wolf nocturnality described in the Main text,[28] because our wolf data were included in this survey. Accordingly, we used the definition of day and night described in the survey paper, which pertains to the start and end of civil twilight[28] (that thus varied with the shifting day length over the 15 study weeks), and we performed comparable analyses to those used in the survey paper, in our comparison here of the nocturnality of wolves, their prey and humans.

QUANTIFICATION AND STATISTICAL ANALYSIS

The treatment effects illustrated in Figure 2, and reported in Table S1, were analyzed using Generalized Linear Mixed Models (GLMMs) with playback treatment as the fixed factor, and video file ID (to account for non-independence of responses when there was > 1 individual in a video) and species identity (when analyzing prey) included as random effects; with (A) Ran (yes or no) analyzed using a binomial distribution and logit link function; and (B) Time to Abandon site analyzed using, a zero-truncated negative binomial distribution and logit link function in the case of wolves, or Box-Cox transformed data in the case of prey.[14] Pairwise post-hoc tests contrasting responses among treatments were all corrected for multiple comparisons (Table S1).

To test if the fear of humans in wolves was robust and consistent with respect to whether it was night or day or there was more or less human activity at a site, we evaluated whether there were significant interactions between the magnitude of wolf responses to the playback treatments and either of these variables (diel period, human activity), by conducting comparative likelihood ratio tests between GLMMs with or without an interaction term. Sites were classified as having more or less human activity on the basis of whether human detections at the site were above or below the median across all sites. The results of these analyses (Table S1) demonstrate that the treatment effects illustrated in Figure 2 regarding wolves are representative of their responses both during the night and day and where there is more or less human activity.

To complement and corroborate our GLMMs of the Ran and Time to Abandon site responses of ungulate prey as whole (Figure 2; Table S1), we conducted simple, robust non-parametric tests of the Ran and Time to Abandon site responses of each of the four ungulate prey species considered individually (Table S2).[14] To account for non-independence when there was > 1 individual in a video, we took the mean (Ran) or median (Time to Abandon site) response as representative of the reaction in that video,[14,20] as described above. We used Fisher’s two-tailed exact tests to evaluate treatment effects on the percentage of trials in which prey Ran, and Mann-Whitney *U*-tests to assess treatment effects on the Time to Abandon site.[14]

To compare the nocturnality of wolves and their ungulate prey (as a whole [“All prey”] and as individual species), with that of humans and dogs, we conducted GLMMs comparing night vs. day detection rates between species (e.g. wolves vs. humans), with ABR site and sampling week included as random effects, to account for potential effects of spatial and temporal variation in human (or dog) activity (Table S3). Note that what is plotted regarding “All prey” in Figure 3 is the percentage of nocturnal detections considering all ungulate detections as a whole, regardless of species. To complement and corroborate the contrast in nocturnality between wolves and their prey compared to humans (and dogs), we conducted simple, robust non-parametric Fisher’s two-tailed exact tests of night vs. day detections between species, to evaluate if there were significant differences in nocturnality between wolves and their prey (as a whole [“All prey”] and as individual species; Table S3).[14]