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Fear of the human "super predator" pervades the South African savanna

Highlights

- Lions have been viewed as the world's most fearsome predator, the "king of beasts"

- New global surveys show humans kill prey at much higher rates than other predators

- Fear of humans vs. lions was tested in iconic savanna mammals from elephants on down

- Fear of the human "super predator" far prevails over that of the "king of beasts"

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In brief

Zanette et al. experimentally show that fear of humans far exceeds that of lions throughout the mammal community in a premier African protected area; strengthening the evidence that fear of the human "super predator" pervades the planet. Paramount fear of humans adds to our global environmental impacts as fear itself can reduce wildlife numbers.

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Fear of the human "super predator" pervades the South African savanna

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SUMMARY

Lions have long been perceived as Africa's, if not the world's, most fearsome terrestrial predator,[1–9] the "king of beasts". Wildlife's fear of humans may, however, be far more powerful and all-prevailing[1,10] as recent global surveys show that humans kill prey at much higher rates than other predators,[10–12] due partly to technologies such as hunting with dogs or guns.[11,13–15] We comprehensively experimentally tested whether wildlife's fear of humans exceeds even that of lions, by quantifying fear responses[1] in the majority of carnivore and ungulate species (n = 19) inhabiting South Africa's Greater Kruger National Park (GKNP),[9,15–17] using automated camera-speaker systems[9,18] at waterholes during the dry season that broadcast playbacks of humans, lions, hunting sounds (dogs, gunshots) or non-predator controls (birds).[9,19–22] Fear of humans significantly exceeded that of lions throughout the savanna mammal community. As a whole (n = 4,238 independent trials), wildlife were twice as likely to run (p < 0.001) and abandoned waterholes in 40% faster time (p < 0.001) in response to humans than to lions (or hunting sounds). Fully 95% of species ran more from humans than lions (significantly in giraffes, leopards, hyenas, zebras, kudu, warthog, and impala) or abandoned waterholes faster (significantly in rhinoceroses and elephants). Our results greatly strengthen the growing experimental evidence that wildlife worldwide fear the human "super predator" far more than other predators,[1,19–28] and the very substantial fear of humans demonstrated can be expected to cause considerable ecological impacts,[1,6,22–24,29–35] presenting challenges for tourism-dependent conservation,[1,36,37] particularly in Africa,[38,39] while providing new opportunities to protect some species.[1,22,40]

RESULTS AND DISCUSSION

Lions kill and inspire fear (anti-predator behavioral responses[1]) in everything from elephants (1,600 kg) to steenbok (8 kg), every other large carnivore and mesocarnivores alike.[2–9] Fear itself has been repeatedly demonstrated to amplify the ecosystem-level impacts of predators by reducing prey population growth rates[29,30] and causing trophic cascades,[6,31–34] in experiments on free-living wildlife in the past decade.[1] Fear of humans has also now been demonstrated to cause cascading impacts from carnivores to ungulates and rodents to plants[1,22–24,35] in experiments that simply broadcast playbacks of people speaking. As predators, humans and lions have long been direct competitors[14,15,41] and human depletion of the lion's prey has contributed to lion declines,[14] consistent with results from recent global surveys indicating that humans kill prey at much higher rates than other predators,[10–12] which together with our unique ecology as predators (e.g., use of "killing technology"[11]) has been proposed to merit humans being termed a "super predator".[11] Given humanity's unique lethality, the fear humans inspire can be predicted to be more powerful and all-prevailing in wildlife communities than even the fear of lions, and thus have even greater ecological impacts,[1,10] but these expectations remain experimentally untested.[1]

South Africa's Greater Kruger National Park[9,16] (GKNP) is one of Africa's premier protected areas and possesses one of the world's largest remaining lion populations.[15,17] Though protected, illegal, and some legally sanctioned, hunting occurs, commonly employing barking dogs to drive prey toward hunters armed with manual weapons or using guns.[13–15] Lions here typically kill prey at waterholes, and hunters often also do so.[3,42,43] Our experiment entailed animals at waterholes hearing in close proximity (∼10 m) either lions (snarling and growling), humans (women and men speaking calmly in locally used languages[44]), hunting sounds or non-predator controls, all broadcast at the same volume (60 dB), following a well-established protocol[9,20–23,25] (see STAR Methods for details).
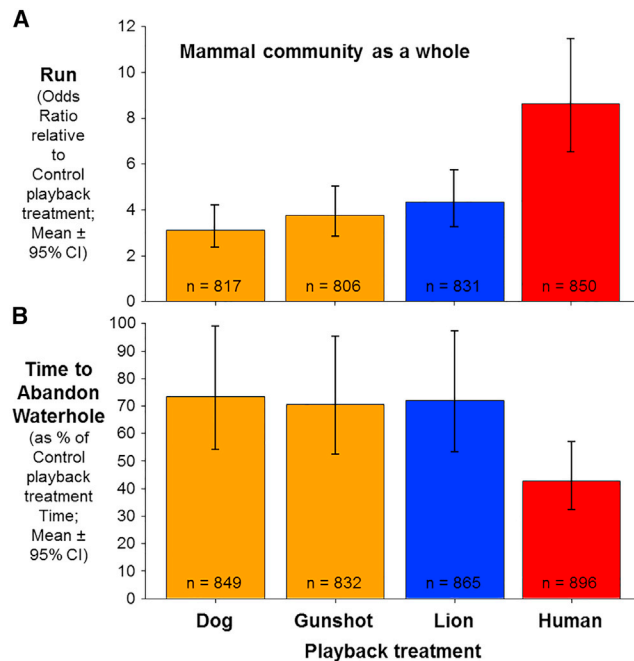
Figure 1. Fear of humans far exceeded that of lions, dogs, or gunshots throughout the savanna mammal community

Across the community as a whole (Table S1), fear of humans significantly exceeded the fear of lions gauged by (A) the greater odds of running (p < 0.001) and (B) shorter time taken to abandon waterholes (p < 0.001) upon hearing humans. Fear of directly hearing human vocalizations, gauged by both measures (A) and (B), also significantly exceeded that of hearing hunting sounds (dogs barking or gunshots; all p < 0.001); the fear of hunting sounds being less than or equal to the fear of lions. Illustrated are effect sizes (means ± 95% confidence intervals [CI]) relative to hearing non-predator controls (birds), which elicited significantly weaker responses than all other treatments (all p ≤ 0.001), corroborating that all others did provoke fear. The n in each bar indicates the number of "independent exposure bouts" (see STAR Methods for details). Control treatment: Run, n = 755; and Time to Abandon Waterhole, n = 796. Full model results and values for each treatment are reported in Table S2.

Fear of humans prevails throughout the community

Fear of humans significantly exceeded the fear of lions throughout the savanna mammal community. Considering the community as a whole (Table S1), wildlife were twice as likely to run (Figure 1A; p < 0.001), and abandoned waterholes during the dry season in 40% faster time (Figure 1B; p < 0.001), upon hearing humans compared with hearing lions (for full model results see Table S2). Critically, this more powerful and all-pervasive response was specifically to hearing human vocalizations, as this differed significantly from all other treatments (all p < 0.001), whereas the responses to hunting sounds (dogs barking or gunshots) were weaker than, or on a par with, those to lions (Figure 1; Run from dogs < lions, p = 0.038; all other hunting sound vs. lion comparisons, p > 0.287; Table S2). Hearing lions or hunting sounds did inspire fear as the responses to these treatments all significantly differed from the control treatment (birds, all p ≤ 0.001; Table S2).

The overwhelming pervasiveness of the greater fear of humans is evident from the fact that fully 95% of species (n = 18 of 19) were either more likely to run or abandoned the waterhole
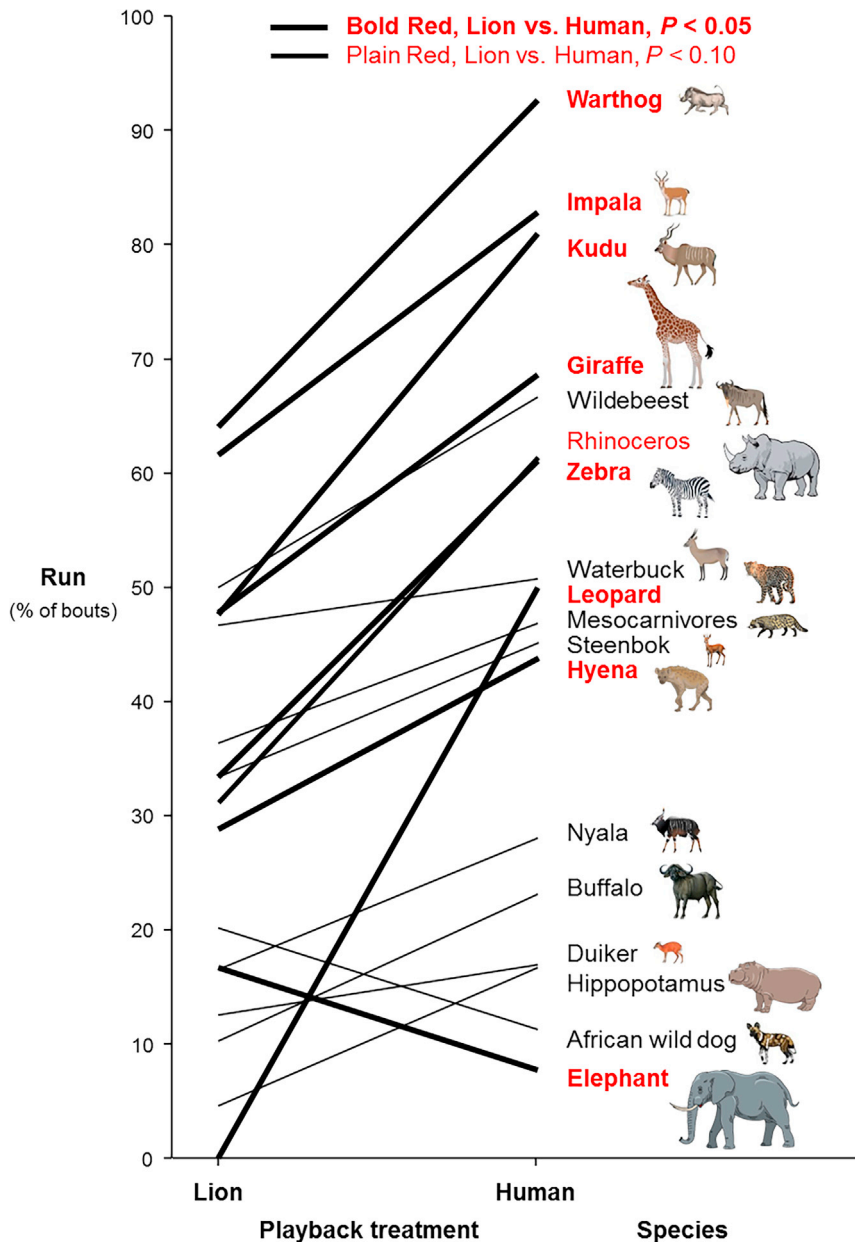
faster upon hearing humans than upon hearing lions (Figures 2 and 3). Substantiating the pervasiveness of this greater fear of humans across all species, both running more or abandoning faster upon hearing humans compared with lions were significant (Run, χ^2_1 = 10.9, p < 0.001; Abandon, χ^2_1 = 8.9, p = 0.003; Friedman ANOVAs), when each species was weighted equally by conservatively using just a single data point per species representing its typical response to the playback treatment (n = 19; the % of bouts in which it ran, or median time to abandon, for that species; for values see Table S3 and for results from all treatments see Table S4).

The robustness of the greater fear of humans throughout the community is corroborated by the results of a decision tree analysis[45–48] concerning the likelihood of running, which included species, playback treatment (human, lion, or control) and six additional potentially explanatory variables: diel period (day or night), body size-trophic level (mesoherbivore,[6] mega-herbivore [> 1,000 kg][6], mesocarnivore, or large carnivore), trophic level (herbivore or carnivore), body mass (kg), group size (per video), and diet (grazer, mixed grazer, browser, or small or large prey).[6] The decision tree first divided species into 5 clusters based on their overall average likelihood of running (Figure 4), ranging from 61% for warthog, to a low of 14% in a cluster including buffalo, duiker, elephant, hippopotamus, African wild dog, and lion. For 4 of these 5 clusters, representing 68% of species, playback treatment was the sole predictor of running, with running from humans being significantly more likely than from lions (all p < 0.001), and more likely from lions than controls. The robustness of the greater fear of humans was thus unmitigated by any other explanatory variable in the majority of species in the community (Figure 4). In the just described cluster that rarely ran (14% on average), diel period best predicted running (Figure 4), which was more likely during day (16%) than night (11%). In turn, running during the day was more likely (22%) in mesoherbivores (buffalo and duiker), which ran significantly more (p = 0.034) from humans (33%) than lions or controls (16%); whereas at night the animals in this cluster, in contrast, ran significantly more (p = 0.014) in response to lions (18%) than to humans or controls (8%). Observations of elephants were prevalent in this test of nighttime running in this cluster (n = 88 of 296) and running more in response to lions reflects the atypical running response of elephants (Figure 2; Tables S3 and S5), discussed below.

Fear of humans prevails in species individually

Considering each species separately, giraffes, leopards, hyenas, zebras, kudu, warthog, and impala all ran significantly more from humans upon hearing humans compared with lions (Figure 2; Video S1), and rhinoceroses exhibited a similar tendency (p < 0.10; for values and full model results see Table S3). Rhinoceroses abandoned the waterhole significantly faster upon hearing humans (Video S2), as did elephants, hyenas, kudu, warthog, and impala (Figure 3), and zebras and waterbuck tended to as well (Table S3).

Except in elephants, running (Figure 2) and time to abandon the waterhole (Figure 3) were inversely associated, i.e., those that ran also abandoned the waterhole in faster time, and the association between the two responses was significant in all species but leopards, buffalo, and African wild dogs (Table S5).

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Figure 2. Most savanna mammal species (89%) were more likely to run from humans than lions

Plotted are the per species per treatment mean percentage of "independent exposure bouts" (see STAR Methods for details) in which the species ran upon hearing lions or humans. Each species whose name is in bold red text responded significantly (p < 0.05) differently to lions and humans, and each whose name is in plain red text showed a strong tendency (p < 0.10) to do so. Note that how lions themselves responded is not depicted because they never ran to playbacks of lions or humans.

Values and details regarding the analysis of each species' responses are reported in Table S3.

See also Videos S1 and S3 and Tables S1, S4, and S5.

For most species (79%), the cost of running was thus significantly compounded with the cost of abandoning a water source. Leopards ran significantly more from humans than lions (Figure 2; Video S1), as did buffalo during the day (Figure 4), but neither was significantly likely to abandon the waterhole to any treatment (Figure 3; Table S3)—possibly because leopards rely on ambushing prey at waterholes[5] and buffalo are considered particularly water-dependent.[3,42,49,50] As regards African wild dogs, there were too few videos of them recorded (Table S1) and their responses were too variable to reveal any significant patterns or effects.

Elephants abandoned the waterhole significantly faster (p = 0.016) upon hearing humans compared with lions (Figure 3; Video S2; Table S3). Elephants are heavily dependent on water, generally drinking daily, and their abandoning the waterhole thus constitutes

a considerable cost.[51] Uniquely, running in elephants did not entail abandoning the waterhole because elephants that ran nevertheless stayed significantly longer at the waterhole (p = 0.033; Table S5). Consequently, elephants did not incur a cost of abandoning the waterhole by running significantly more (p = 0.014) in response to lions than humans (Figure 2; Table S3). In most cases when elephants ran (79%) there were multiple videos of them recorded in a bout because they either ran a few meters and stopped or ran out of view but then returned. Running but then staying longer reflects running often being defensive or even offensive in elephants,[4,44,52] rather than evasive as in most other species. Correspondingly, upon hearing lions, elephants on multiple occasions either: ran toward each other in a defensive "bunching" response before approaching as a group, as described in previous lion playback experiments on elephants and consistent with elephants often cooperatively aggressively defending against lions[4,44,52]; or they ran toward and aggressively attacked the speaker playing lion vocalizations (Video S3). Critically, such reactions were never observed when elephants heard humans. Though lions can kill immature elephants, adult elephants are able to effectively defend against lions,[4,52] whereas the same is not true of attacks by humans.[10–12,14,41,44] Accordingly, rather than attempt to defend themselves, elephants retreated from the waterhole significantly more rapidly upon hearing humans in our experiment (Figure 3; Video S2), just as they similarly retreated significantly often after hearing humans in a prior playback experiment,[44] highlighting that even elephants fear humans more than lions.

Ecological and conservation significance

The ecological and conservation significance of our experimental results has five critical facets. First is the very substantial
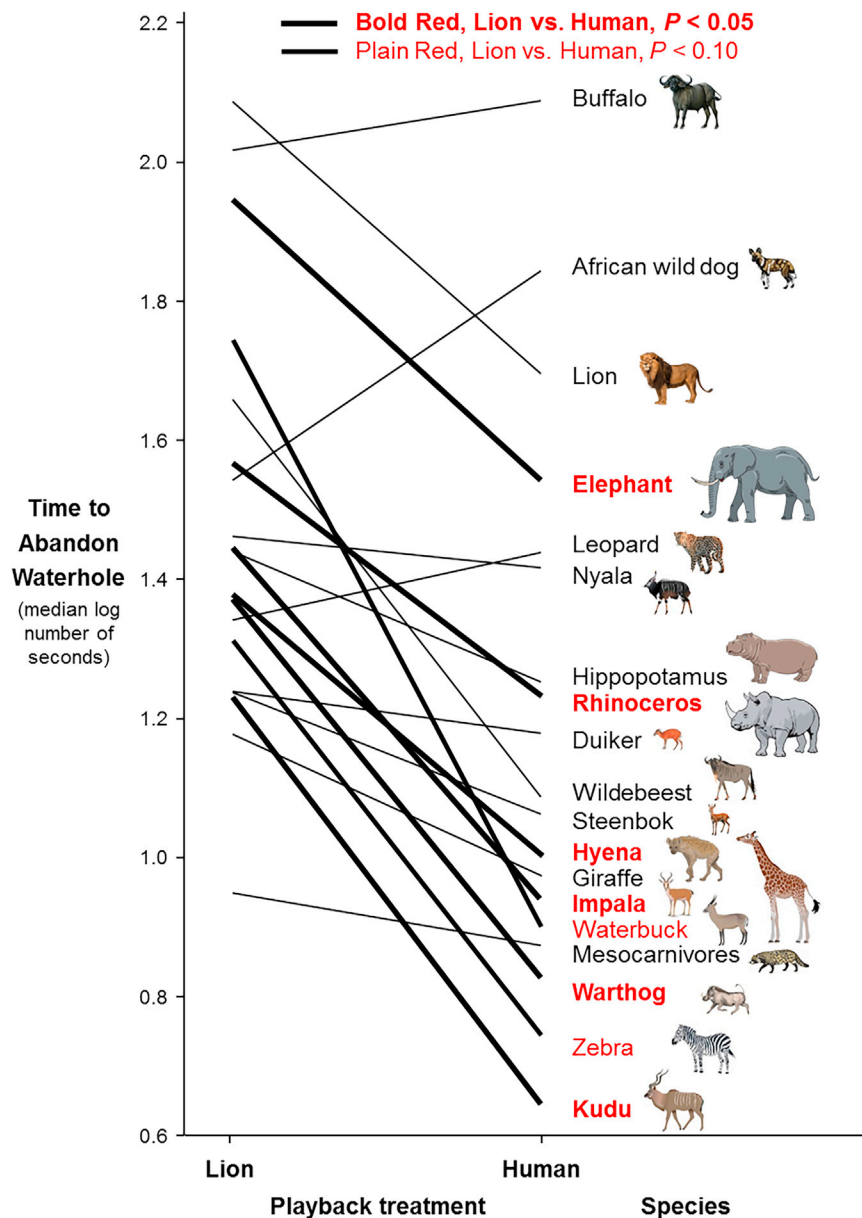
Figure 3. Most savanna mammal species (84%) abandoned waterholes faster upon hearing humans compared with lions

Plotted are the per species per treatment median time to abandon a waterhole upon hearing lions or humans. Each species whose name is in bold red text responded significantly (p < 0.05) differently to lions and humans, and each whose name is in plain red text showed a strong tendency (p < 0.10) to do so. Values and details regarding the analysis of each species' responses are reported in Table S3. See also Videos S2 and S3 and Tables S1, S4, and S5.

the collection of thousands of experimental trials on diverse species in a relatively short time without the need of having a human observer present[18,36] (see STAR Methods for details).

The strength, comprehensiveness, and context of these results from Africa greatly augment the growing experimental evidence from this and similar recent playback studies in North America, Europe, Asia, and Australia,[1,19–28] which is demonstrating that wildlife worldwide fear humans far more than other predators, consistent with the global surveys documenting humanity's greater lethality.[10–12] The similar experiments have demonstrated that mountain lions,[20,23,24] multiple species of deer[21,22,26] and mesocarnivores,[19,24,28] kangaroos and wallabies,[25] and wild boar[27] all fear humans far more than the non-human apex predator in the system, including leopards, wolves, bears, cougars, and dogs. Our results now demonstrate that this greater fear of the human "super predator" exceeds even that of the "king of beasts" (lions) and can pervade entire communities of mammals, even in protected areas.

Darwin discussed fear of humans in wild animals in *The Voyage of the Beagle*,[53] so this notion is not unprecedented.[1] What is new is the comprehension of the great degree and pervasiveness of this fear and the burgeoning experimental evidence that fear itself can have significant ecological impacts.[1] The very substantial degree to which wildlife fear humans is being revealed with far greater clarity thanks to the new experiments now capable of quantifying the relative fear of humans because they include both positive (fearsome; e.g., large carnivore) as well as negative (non-predator; e.g., bird) controls.[1,36] The pervasiveness of wildlife's fear of humans is being revealed by its global and contextual extent. In addition to being experimentally demonstrated on five continents, pervasive fear of humans has been proposed to explain why mammals worldwide modify their movements and nocturnality in proximity to humans.[1,24,54,55] Pervasive fear of humans has, moreover, now been experimentally demonstrated in

degree to which fear of the human "super predator" exceeds that of Africa's,[2–9] if not the world's (given its size and group hunting[9]) most fearsome large carnivore, the lion (Figure 1). Second is the comprehensiveness with which this greater fear of humans pervaded the community of savanna mammals (Figures 2 and 3), inhabiting one of the world's premier protected areas.[9,15–17] Third is that this is occurring where fear of lions can be expected to be maximal because this is home to one of the world's largest remaining lion populations,[15,17] and waterholes are where the danger from lions is greatest.[42] Fourth is that it was specifically hearing human vocalizations which inspired the greatest fear (Figure 1), suggesting that wildlife recognize humans as the real danger, whereas related disturbances such as barking dogs are merely lesser proxies.[1,19–22,25,26] Fifth is that our automated methodology enabled

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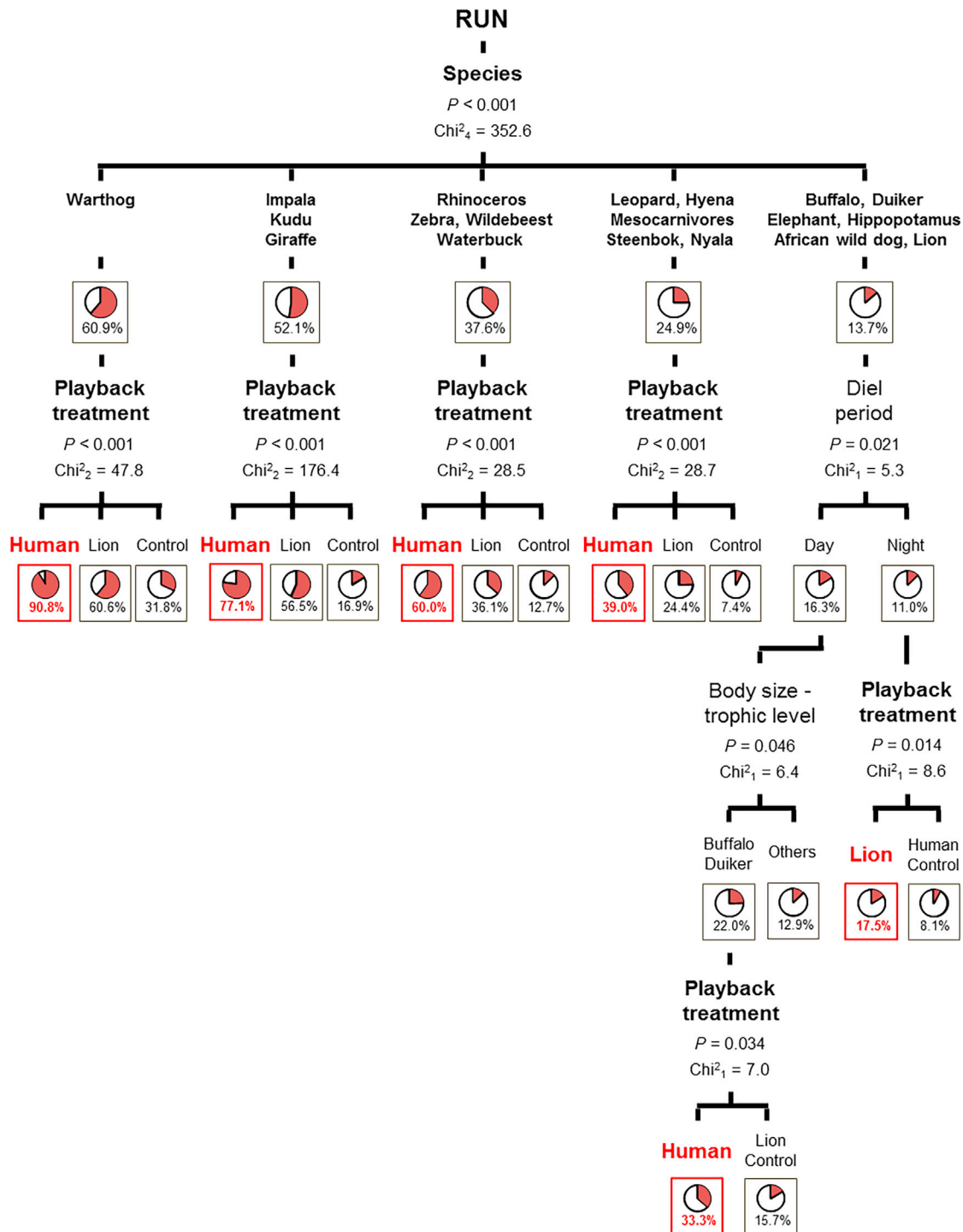
Figure 4. Unmitigated fear of humans best predicted running in most savanna mammal species (68%)

Depicted is the decision tree produced by a classification tree analysis[45–48] (see STAR Methods for details) conducted to determine which of eight potentially explanatory variables best predicted running in the savanna mammal community: species identity, playback treatment (human, lion, or control), diel period, body size-trophic level, trophic level, body mass (kg), group size, or diet. The first branch simply clustered species based on their natural proclivity to run. In all species with all but the minimum natural proclivity to run (4 of 5 clusters, which included 68% of species), the sole best predictor of running was hearing humans, unmitigated by diel period, body mass, group size, or any other potentially explanatory variables. Hearing humans significantly predicted running in two more species, buffalo and duiker (for a total of 79% of all species), but this was mitigated by whether it was day or night (2nd branch in tree) and their being

(legend continued on next page)

protected areas (this study and Liu et al.[27]) and urban settings,[19,28] where wildlife may appear to be habituated to humans. Experimental testing is both feasible[19,23,24,28] and essential in order to draw strong inferences concerning apparent habituation to humans or the relative fear of us, because human occupation of resource-rich areas and access to anthropogenic resources such as refuse, livestock, and crops means wildlife can be expected to co-occur with us, despite their fear of us.[1,24,28,36,56]

The significantly greater fear of human vocalizations than hunting sounds (dogs barking, gunshots) demonstrated in our experiment (Figure 1) has clear conservation implications because this indicates that wildlife perceive human presence per se as malignant and a more immediate signal of danger than disturbances associated with lethal human activities.[1,36] Greater fear of humans than gunshots has not been demonstrated before, but greater fear of humans than dogs has been repeatedly.[19–22,25,26] If wildlife do not differentiate between humans engaged in benign or lethal activities, e.g., photographic tourism vs. hunting, then the very considerable ecological impacts now demonstrated to be caused by the fear of humans[1,22–24,35] can be expected to result from exposure to even benign humans.[1,36] Whereas area closures and other restrictions on tourism to minimize exposure of wildlife to humans for conservation purposes have been implemented in taxpayer-funded protected areas in wealthy countries,[57] such restrictions pose a management dilemma in African protected areas that are largely reliant on gate receipts from wildlife tourists for their funding.[38,39] The presence of a predator in close proximity is what inspires fear,[1] whether heard, seen, or smelled, so this is not solved by simply asking tourists to be quiet. Gauging if fear of humans is having undesirable impacts must first be experimentally tested and our automated methodology provides one means of cost-effectively doing so.[18,36] If fear of humans appears to be a problem, one possible way to ameliorate this is to actively habituate wildlife to humans, as done to promote gorilla tourism in several African protected areas, but this process can take years[37] and habituating other wildlife may be equally challenging. New, ideally automated, methods to accelerate this are clearly needed.[18,36]

Generalized fear of humans, although potentially presenting a challenge for wildlife tourism, provides an opportunity with respect to protecting wildlife from illegal hunting. Automated methods to accomplish this are now available as recent experiments have demonstrated that playbacks of human vocalizations can deter wildlife from occupying large areas (km^2) over prolonged periods (16 weeks) at low cost.[22,24,28–30,33,34,40] Our finding that rhinoceroses ran and abandoned waterholes upon hearing humans (Figures 2 and 3; Video S2) shows that this technique could be used to deter rhinoceroses from occupying areas where they are at most risk from poaching,[40] which has increased exponentially in GKNP since 2008.[58] Our results and those from the similar experiments discussed[19–22,25,26] demonstrate that specifically hearing human vocalizations—rather

than barking dogs, for example—can generally be expected to be the most effective deterrent to use to safeguard most species of wildlife.[1,22,36]

If paramount fear of the human "super predator" pervades the planet, as increasingly indicated, this adds a new dimension to our worldwide environmental impacts,[1,10] given it is also now evident that fear itself can significantly reduce wildlife numbers.[1,29,30] Measuring, mitigating, and manipulating the fear we inspire in wildlife presents challenges and opportunities, which we suggest ought to now be considered integral components of conservation planning and protected areas management.

STAR★METHODS

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

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  - Quantifying fear responses
- QUANTIFICATION AND STATISTICAL ANALYSIS

AUTHOR CONTRIBUTIONS

L.Y.Z., M.C., and C.P. designed research; all authors performed research; L.Y.Z., N.R.F., and M.C. analyzed data; and L.Y.Z., M.C., and C.P. wrote the paper with input from all other authors.

mesoherbivores (3rd branch). In the species in the cluster with the minimum proclivity to run (14%), which included buffalo, duiker, elephant, hippopotamus, African wild dog, and lion, these species ran even less at night (11%; 2nd branch), but if they did, they ran most to lions (3rd branch), which is likely attributable to the atypical running response of elephants (Figure 2; Video S3; Tables S3 and S5), observations of which predominated here.
See also Table S1.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Processed video data	Lead contact	lzanette@uwo.ca
Software and algorithms		
SPSS	IBM Corp.	Version 28.0.1

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.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Study area, sites and subjects
The GKNP comprises Kruger National Park and the adjoining Associated Private Nature Reserves[16] where we conducted our experiment.[9] Adjoining GKNP on the east is Mozambique's Limpopo National Park. Wildlife are free to roam this vast area (ca. 32,500 km^2) as only the western perimeter of the GKNP is fenced.[15,16] The experiment was conducted at 21 waterholes (each > 2 km apart) over 6 weeks during the dry season (June–August). The 21 waterholes lay within a 21 km radius of 24.364° S and 31.164° E and encompassed an area of at least 240 km^2 of contiguous savanna.

We deployed one automated camera-speaker (Automated Behavioural Response; ABR) system[18] per waterhole which operated 24 h/day without any human presence, video-recording the responses of animals to the playback treatments.[9] The subjects were thus any and all wildlife visiting one of the 21 waterholes that triggered the ABR there. We recorded the responses of 26 species of ungulates and carnivores (Table S1). In the Main text and Figures 2, 3, and 4 we refer to n = 19 species, comprising 18 individual species plus 8 species collectively identified as "mesocarnivores". Prior playback experiments on other continents[19,24,28] have reported mesocarnivores demonstrating significant fear of humans so their reactions were of specific interest. To address this we pooled and analyzed the responses of all mesocarnivore species collectively as there were too few videos recorded of each (Table S1).

We recorded a total of n = 4,238 "independent exposure bouts", following the definition of an "independent exposure bout" well-established 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.[9,20–22,25] Note that this is more conservative than the > 30 min used to define independent occurrences in most camera trap studies.[21,22,25] We recorded 10,720 videos over 764 camera-trap-days (24 h periods) across the 21 waterholes. The median, mean and maximum number of videos per "independent exposure bout" were 1, 2.5 and 39 respectively. The median and mean number of "independent exposure bouts" per waterhole corresponded closely (median = 195; mean ± SD = 202 ± 105), and the distribution across waterholes was normal with one outlier with 534 bouts. Table S1 reports the number of "independent exposure bouts" per species, which together with the number of videos per bout and the distribution of bouts among waterholes is indicative of the number of subjects sampled and their exposure to the treatments.

This research adhered to the *Canadian Council on Animal Care guidelines: Wildlife* (https://ccac.ca/Documents/Standards/Guidelines/CCAC_Guidelines-Wildlife.pdf) and was approved by the Western University Animal Care Committee. As this was a camera-trapping experiment on free-living wildlife the subjects comprised whatever species, number, sex or age of animal visited a waterhole and triggered the ABR. The diversity of species (Table S1) meant only a portion were sexually dimorphic and only a portion

were accompanied by recognizable young at this time of year. Consequently, since sex and age were not classifiable in all species these were not included in analyzing the community-level questions addressed here.

Experimental rationale and design

Contrasting the fear inspired by humans compared to lions represents a critical test of the paramountcy of wildlife's fear of the human "super predator". The voluminous evidence of the fear lions inspire[2–9] and the many similarities lions and humans share as predators means it is readily conceivable that lions could be more feared than humans. Outside the lion's range there are reasons to expect that greater relative and more pervasive fear of humans prevails. Lions are the second largest and most social felid,[2] and their size and group hunting enable them to kill virtually every other mammal, including even immature elephants.[2–9] Lions are obviously larger than humans, but humans are as large as, or larger than, every extant carnivore on the African savanna, and our relatively large body size and group-hunting strategies have similarly contributed to humans being able to kill every other mammal, including even adult elephants, since at least the late Pleistocene.[10–12,14,41] Being large and social, both lions and humans are very vocal,[15] facilitating the use of playbacks of their vocalizations to compare the fear each inspires.[9] Paramount fear of humans is plausibly more likely to prevail outside the lion's range (Africa, the Middle East and parts of India[59]) because humans have for millennia been the largest group-hunting terrestrial predator everywhere else,[41] and evidence from one of the recent global surveys of humanity's greater lethality indicates that contemporary hunters in North America and Europe exploit prey at considerably higher relative rates than hunters in Africa.[11]

At present, hunting in African savanna systems is largely conducted using dogs, guns or snares.[13–15] Hunting even elephants using dogs dates back many millennia.[41] Barking dogs are used to drive prey to locations where the human hunters can more easily kill them.[13,15,41] Guns are used in legal hunting and culling as well as in illegal hunting.[13] Laws against gun ownership cause some illegal hunters to use dogs to avoid the sound of gunshots.[13,14] Whether it is the sound of barking dogs or gunshots it can consequently be assumed savanna mammals recognize and associate these with lethal human hunting. Though snares do not make noise animals may learn that hearing humans is linked to this source of lethality. Lions visit snaring hotspots,[60] attracted by prey distress calls[61] and the opportunity to kill or scavenge snared prey,[13,15,60] and the presence of distressed or dead individuals caught in snares is an equally clear signal to prey that danger lurks there.[1,7] Hunters must repeatedly visit to set and check their snares providing the opportunity for prey to associate humans with this danger.[62] Whether hunting is conducted using dogs, guns or snares, wildlife may recognize that human presence is the common feature signifying imminent peril.[1,19–28]

All five playback treatments (lions, humans, dogs, gunshots and non-predator controls) were broadcast at each of the 21 waterholes. 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 behavior, e.g., a walking animal starts to run demonstrating that it is reacting to the playback.[9,18] If an animal remained in front of the camera and triggered it again another playback would be broadcast. Prior ABR experiments have also shown that reactions to repeated exposures to the same treatment provide a further measure of fear; specifically, while an animal attracted by bait (e.g., a waterhole) might run a few steps to any sudden sound, it can be expected to stay, and remain longer, and so be exposed to multiple playbacks of the same treatment, the less frightening the treatment.[20–23] This is the basis of our "time to abandon waterhole" measure (defined below). As in prior ABR experiments,[21,22,25] to optimize capturing reactions to both, repeats of the same treatment, and different treatments, the treatment broadcast if the ABR was triggered changed every 16 min, i.e., not too frequently or infrequently. To illustrate, if triggered any time between 00:00 and 00:16 a.m. one treatment would be broadcast, e.g., lions, between 00:16 and 00:32 a different one would, e.g., humans, and so on.[21,22,25] To ensure the broadcast of treatments was balanced and randomized across the diel cycle each ABR was programmed to broadcast all five treatments in random order, and then do so again in a different random order while avoiding broadcasting the same treatment for > 16 min, and so on, until the whole 24 h cycle was accounted for.[21,22,25] Prior to use we verified that each programmed sequence was free of potential order effects. Note that the number of "independent exposure bouts" was generally balanced across all five treatments (Table S1) as intended by our sampling design.

We used 8–14 exemplars of each playback treatment to ensure responses were to the type of sound (e.g., human vocalizations) rather than to the specifics of a particular exemplar.[19] Playbacks were standardized to a volume of 60 dB at 10 m so as to be audible, but not startling, to animals within the 15 m detection range of the camera's motion sensor.[9,19–23,25] Human exemplars consisted of individuals speaking Tsonga, Northern Sotho, Afrikaans or English, calmly in a neutral fashion not conveying alarm or threat, to simulate overhearing people speaking in conversation.[19–23,25] Lion snarls and growls were similarly broadcast to simulate lions in 'conversation' rather than roaring at each other.[9] A previous ABR experiment in the GKNP demonstrated that the ungulate community responded significantly fearfully to these lion vocalizations and responded significantly more fearfully to them than to African wild dog or cheetah vocalizations.[9] To comprise an optimal, non-threatening control composed of familiar, benign heterospecific animal vocalizations, we used the vocalizations of three locally abundant bird species, the African Hoopoe (*Upupa africana*), Pearl-Spotted Owlet (*Glaucidium perlatum*), and African Wood Owl (*Strix woodfordi*), broadcast during diel, crepuscular, and nocturnal hours, respectively, as done using bird vocalizations as controls in prior ABR experiments.[9,21,22] Bird vocalizations were designed to constitute a single treatment (controls) and treated as such in our analyses.[9,21,22,29,30] Each time the ABR was triggered the above described programmed sequence determined the treatment broadcast but which exemplar of that treatment was played was randomly selected.[9,21,22,25]

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METHOD DETAILS

Field procedures

At each of the 21 waterholes we created a consistent 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.[9,18,20–23,25] First, we located a tree 10 m from a track running parallel to the water's edge. We then strapped the ABR's camera to the tree at a height of 1.5 m and positioned the connected speaker 0.5 m directly above the camera. Next, we set the focal point of the camera such that its line of sight intersected the track along the water's edge at a distance of 10 m. Following this we clipped vegetation within a 15 m radius in front of the camera to reduce false triggers and ensure 100% detection at 10 m.[9,18] Finally, to prevent animals from simply showing a startle response to hearing any sound at too close a range, we corralled them away from the immediate vicinity of the ABR by piling thorny *Acacia* cuttings and woody debris in a 5 m radius around the tree with the ABR.[9,18] Targeting the camera at a point 10 m distant meant even elephants were encompassed within the camera's field of view, and corralling animals between the water's edge and *Acacia* barrier meant most animals were 10 m away and in the center of the camera's field of view when the playback broadcast, ensuring their reactions were clearly and readily quantifiable[9,18] (Videos S1, S2, and S3).

Quantifying fear responses

We quantified (A) whether animals ran in response to a playback because running (fleeing) is among the most straightforward behavioural measures of fear[1] and was readily recognizable in every species.[9] We operationally defined running as taking more than three consecutive rapid steps.[9] 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.[9,21,25] We quantified (B) "time to abandon waterhole" by calculating the time elapsed between the start of the playback in the first video in each "independent exposure bout" and either: i) the last time the animal was in view, or the video ended, if there was just one video in the bout; or ii) the start of the last video in the bout.[21,22] To illustrate, if an animal heard a playback and left the camera's field of view 15 s later and there was just one video in the bout the "time to abandon waterhole" would be 15 s; whereas if an animal heard a playback in the first video and was then recorded hearing the same treatment in a second video 2 min later and a third video after another 2 min, and then not recorded hearing that treatment for > 60 min after that, the "time to abandon waterhole" would be 4 min. 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 median response as representative of the reaction in that video.[9,22] 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).[9]

QUANTIFICATION AND STATISTICAL ANALYSIS

The whole-community level results illustrated in Figure 1 were analyzed using Generalized Linear Mixed Models (GLMM; full model results Table S2) with playback treatment as the fixed factor, species identity and waterhole number as random effects, and the number of days of ABR deployment at a given waterhole as a covariate (to account for possible habituation); with (A) Running analyzed using a binomial distribution (yes or no) and logit link function; and (B) Time to Abandon the Waterhole analyzed using Box-Cox transformed data. Figure 1 illustrates effect sizes based on these analyses. The p values concerning pairwise contrasts reported in the Main text are from sequential Bonferroni pairwise post-hoc tests comparing responses among all five playback treatments (Table S2). Our GLMMs were conservative in using the Satterthwaite approximation for designs with unequal sample sizes (e.g., per species), and the robust procedure.[63] All statistical analyses were conducted using SPSS V28.0.1.[63]

In addition to including species identity in our GLMMs we sought to exhaustively evaluate the overall pervasiveness of the greater fear of humans by explicitly addressing how many species demonstrated this response and the existence of any exceptions (e.g., the atypical running response in elephants; Figure 2). To complement our comprehensive GLMMs we thus conducted simple, robust and conservative Friedman repeated-measures ANOVAs comparing each species' response to humans with its response to lions (reported in the Main text) and all other treatments (Table S4). Time to abandon the waterhole was not normally distributed in any species so we used the median time to abandon (Figure 3; Table S3) to characterize each species' typical response in these ANOVAs.

Decision (or "classification") tree analysis is a non-parametric method that uses a recursive algorithm to decide which or what combination of potentially explanatory variables best predicts the value of a response variable.[45–48] We used the "exhaustive CHAID" algorithm to construct our decision tree and cross-validated it using 10 sample folds, which is considered robust.[47,63] As described in the Main text, the goal of our decision tree analysis was to evaluate the robustness of the greater fear of humans, which could be most straightforwardly tested by simply considering running in response to humans compared to lions, given that running to lions was greater than to hunting sounds (Figure 1A) and the greater fear of humans was generally equally well reflected by either running or abandoning (Figures 1, 2, and 3; Table S3).

We tested the running response to humans vs. lions in each species separately (Figure 2; Table S3) by treating run as a binomial (yes or no) and conducting GLMMs or logistic regressions with or without waterhole number (random) or ABR days (covariate) in the model, or Firth logistic regressions,[64] depending on what best suited the species (Table S3). To complement our comprehensive tests of running, we tested the time to abandon the waterhole to humans vs. lions in each species using simple, robust Mann-Whitney *U*-tests (Figure 3; Table S3). Both measures (ran, abandoned) and the different statistical procedures used (GLMMs, regressions or *U*-tests) generally provided the same answer regarding each species' greater fear of humans (Tables S3). We tested the association

between running and abandoning in each species by comparing the time to abandon the waterhole between bouts in which the species did or did not run, by again using simple, robust Mann-Whitney U-tests (Table S5). Because the atypical running response of elephants (Figure 2; Video S3; Tables S3; S5) meant their greater fear of humans was wholly revealed by their abandoning the waterhole significantly faster upon hearing humans (Figure 3; Video S2; Table S3), we conducted a repeated-measures test comparing the time to abandon in response to humans vs. lions at each waterhole (Wilcoxon matched-pairs test, $T_{18} = 31.0$, p = 0.018), which verified that their significantly faster abandoning in response to humans was robust to variation among waterholes.