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Journal

Proceedings of the Royal Society B, 284(1857)

ISSN

0962-8452

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Publication Date

2017-06-28

DOI

10.1098/rspb.2017.0433

Peer reviewed



Research

Cite this article: Smith JA, Suraci JP, Clinchy M, Crawford A, Roberts D, Zanette LY, Wilmers CC. 2017 Fear of the human 'super predator' reduces feeding time in large carnivores. *Proc. R. Soc. B* **284**: 20170433. <http://dx.doi.org/10.1098/rspb.2017.0433>

Received: 28 February 2017
Accepted: 19 May 2017

Subject Category:
Behaviour

Subject Areas:
behaviour, ecology

Keywords:
ecology of fear, indirect effects,
playback experiment, *Puma concolor*,
risk–foraging trade-off, trophic cascade

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Fear of the human 'super predator' reduces feeding time in large carnivores

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Large carnivores' fear of the human 'super predator' has the potential to alter their feeding behaviour and result in human-induced trophic cascades. However, it has yet to be experimentally tested if large carnivores perceive humans as predators and react strongly enough to have cascading effects on their prey. We conducted a predator playback experiment exposing pumas to predator (human) and non-predator control (frog) sounds at puma feeding sites to measure immediate fear responses to humans and the subsequent impacts on feeding. We found that pumas fled more frequently, took longer to return, and reduced their overall feeding time by more than half in response to hearing the human 'super predator'. Combined with our previous work showing higher kill rates of deer in more urbanized landscapes, this study reveals that fear is the mechanism driving an ecological cascade from humans to increased puma predation on deer. By demonstrating that the fear of humans can cause a strong reduction in feeding by pumas, our results support that non-consumptive forms of human disturbance may alter the ecological role of large carnivores.

1. Introduction

Humans have assumed the role of 'super predator' in animal communities globally, killing terrestrial carnivores at rates as much as nine times higher than their natural predators [1]. In addition to directly killing large carnivores, humans might also elicit fear responses in these species as they do in other wildlife taxa that experience human-caused mortality [2,3]. Indeed, correlative evidence of human-induced changes in large carnivore space use and movement suggests that fear of humans is a common phenomenon among top predators [4–8]. However, it has yet to be experimentally tested if large carnivores perceive humans as predators and whether changes in large carnivore behaviour caused by fear of humans affects ecological communities.

It is increasingly recognized that, even in the absence of direct mortality, fear of predators can itself drive cascading changes across food webs [9,10]. Human-induced fear in large carnivores is likely to have similar cascading effects because of the well-documented top-down effects of large carnivores on their prey and competitors [11–13]. However, different outcomes of human-induced fear in carnivores on prey populations might be expected depending on the nature of the carnivore response. One potential outcome of large carnivore fear of humans is the human shield effect, whereby prey find refuge in human-dominated habitats and are released from top-down forces because carnivores spatially avoid human disturbance [14,15]. However, human disturbance could have the opposite effect on the regulatory role of large carnivores if carnivores persist in human-dominated habitat by instead avoiding humans temporally. This counterintuitive response may actually increase predation pressure on prey by altering carnivore hunting behaviour to accommodate an enhanced risk–foraging trade-off; temporal avoidance could lead to reduced total feeding

time at a kill, which would require increased kill rates to compensate for lost energetic return from each kill. As land is increasingly transformed by anthropogenic development, quantifying how the fear of humans affects interactions between large carnivores and their prey is essential to understanding novel ecological dynamics emerging in human-dominated landscapes [7,11,16].

We previously reported that pumas (*Puma concolor*) in the Santa Cruz Mountains of Central California spent less time at kill sites in more residential areas and increased kill rates of prey [5]. This increased kill rate could potentially be explained by altered prey communities in human-dominated habitats (either from a perceived human shield or access to anthropogenic food subsidies) leading to more vulnerable [17] or available [18] prey. However, if reduced time at kill sites near residential development is fear-induced, it could also result in increased kill rates to compensate for reduced energy gained per individual predation event. Here, we experimentally test whether pumas exhibit fear responses to the human 'super predator' and whether changes in puma feeding behaviour in response to human-induced fear can explain our previously reported differences in puma feeding time and kill rate between areas of high and low human presence in the Santa Cruz Mountains [5]. To our knowledge this is the first direct experimental test of whether large carnivores respond fearfully to human presence, and whether this response has measurable ecological consequences.

To test the relationship between fear of humans and feeding behaviour, we executed a playback experiment on wild pumas. Predator playback experiments have been used to substantiate fundamental ecological relationships [19], including that the fear of predation reduces reproductive success in birds [20], that fear can have cascading impacts on animal communities [10], and that mesocarnivores exhibit heightened fear responses to human 'super predators' relative to non-human predators [3]. However, no study has linked the fear of humans to feeding behaviour in large carnivores. Our study builds on protocols used in over 200 predator playback experiments [19]. Hearing a predator vocalization signals to prey the direct presence of the predator in relatively close proximity, which is why simulating this using audio predator playbacks provides such a powerful means of directly testing fear responses [3,19,21]. Previous experiments have established that prey hunted by the human 'super predator' react to human vocalizations just as prey react to the vocalizations of any other predator [3], demonstrating that assessing responses to human vocalizations provides the means to directly test the prey's perception of humans as predators, rather than humans as simply a source of noise and disturbance (*sensu* [4]). Our experimental approach correspondingly allows us to make direct inferences concerning fear of the human 'super predator' and the resulting consequences of anthropogenic disturbance on risk–foraging trade-offs in a large carnivore. Combined with our previous work [5] our study reveals an ecological cascade from humans to increased predation on deer mediated by fear.

2. Methods

Our experiment was part of a long-term study on puma ecology in the Santa Cruz Mountains of Central California, USA [5,6]. The region has a Mediterranean climate characterized by a

rainy season in winter and dry season in summer. Habitat types include mixed hardwood forest, redwood forest, chaparral and grassland. The Santa Cruz Mountains are heavily impacted by human use, particularly residential development and outdoor recreation. Puma exposure to humans here is thus commonplace; all pumas in this study have housing developments in their home range (mean: 21.7 houses km⁻²) and kill and cache prey as close to 5 m from people's homes [5]. Pumas have a good reason to be fearful of humans in this region, as they were bounty hunted in California for decades and even today humans are their primary source of mortality in the Santa Cruz Mountains (Wilmers unpublished data).

We conducted a playback experiment on pumas at their active kill sites. We first located puma kill sites from recent GPS tracks of collared individuals (IACUC no. WILMC1011). We downloaded recent GPS locations successfully transmitted through GSM or Iridium technologies and identified potential fresh kill sites as clusters of locations within 100 m of one another that occurred between sunset and sunrise. We field-investigated potential kill sites that were no more than 3 days old and at which the puma was present the previous night. If a fresh kill was found, we tied the carcass down so it could not be dragged out of the view of our cameras. Any behavioural effects of tying down the carcass were experienced for both control and experimental playback treatments, therefore baseline disturbance levels should not influence the relative difference in response between treatments.

To test whether pumas fear humans and quantify the cost of this fear, we broadcast predator (human) or non-predator (Pacific tree frog, *Pseudacris regilla*) playbacks at puma kill sites following well-established experimental methods [10,19,20]. Tree frog vocalizations provide an ideal control – like humans, tree frogs occur throughout the study area, but unlike humans they are neither predators, prey, nor competitors of pumas, and thus represent an equally familiar but benign stimulus. Tree frog vocalizations further provide an ideal control because they may naturally be heard both night and day, whenever pumas are active. Controls in other playback studies testing for fear responses in wildlife include running water (study organism: moose; [22]), seals (study organism: raccoon; [10]), sheep (study organism: European badger; [3]) and assorted non-threatening birds (study organism: song sparrow; [20]).

We recorded puma responses to playbacks using an Automated Behavioral Response (ABR) system (i.e. video-enabled camera trap linked to a playback unit triggered by the camera's activation) [21]. We deployed the playback speaker 400–450 cm from the centre of the carcass. Videos were 30 s long, the playback being broadcast for 10 s in the middle of the video. If the puma repeatedly triggered the camera it could hear the playback as often as twice per minute. We used seven exemplars of each playback type [23], the human exemplars all consisting of a single individual speaking conversationally. We edited all exemplars for consistency in amplitude and quality using Audacity® (v. 2.1.0, Audacity Team 2014), and broadcast the playbacks at a consistent peak sound pressure level of 80 dB at 1 m (measured using Radioshack 33-2055 Digital Sound Level Meter set to fast response and C weighting). This volume was chosen to mimic the natural volume of human conversation. Using these exemplars we composed 30 min playlists of each treatment. The playlists alternated between frogs and humans every 30 min; which treatment the puma heard first being determined by when it triggered the camera, and was thus effectively random. An individual puma might be exposed to either or both treatments over 24 h, depending upon its reaction. For pumas that heard both treatments, there was no significant difference in the proportion of each treatment first heard ($Z = 1.63, p = 0.103$). Pumas were exposed to each treatment only once over the course of the study.

We tested for the fear response of pumas and its ecological cost as follows: (i) We examined the puma's initial response to

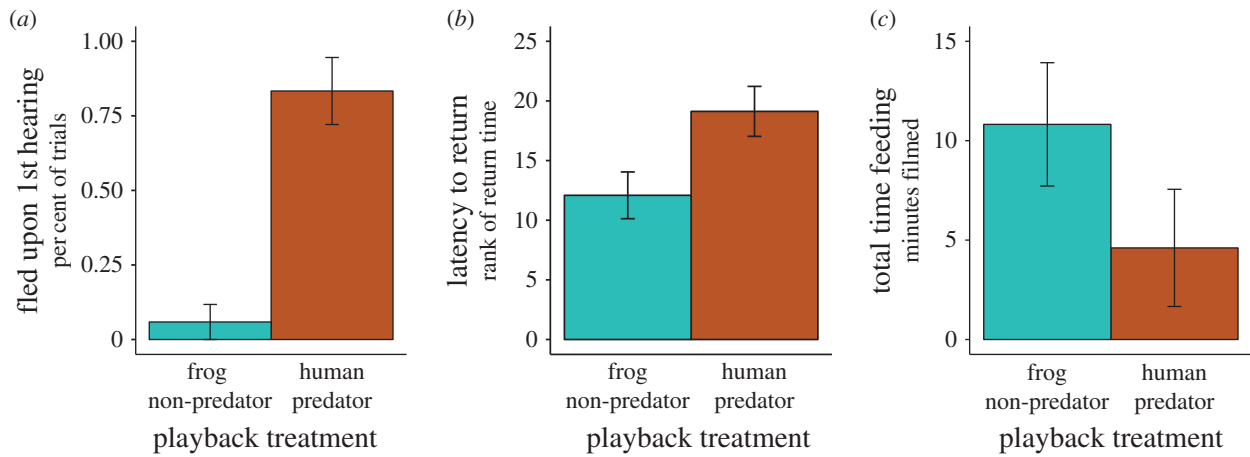


Figure 1. Responses of pumas to predator (human) and non-predator (frog) playbacks at puma feeding sites. (a) Proportion of pumas that fled following their first exposure to frog or human playbacks. (b) Latency in time to return (rank) after initial playback exposure. (c) Total time spent feeding during the first 24 h of playback treatment. Bars represent standard error. Although transformation of feeding data was required to meet normalization assumptions for our analysis, here we show mean and standard error of raw feeding time measures for purposes of visualization. (Online version in colour.)

the playbacks by quantifying whether the puma fled (ran away) upon first hearing a treatment. We tested for significant differences in fleeing using Fisher's exact test. (ii) We assessed recovery time following puma initial exposure to each playback as the time difference between their first exposure to a playback treatment and the next video in which they subsequently appeared (hereafter, 'latency to return time'). We ranked the latency to return time for each trial, assigning the highest rank to individuals who did not return. We tested for a treatment effect by applying a Mann–Whitney U test to the ranked return times. Some pumas were exposed to both treatments enabling us to additionally test these two responses (fleeing and latency) using repeated-measures Wilcoxon matched pairs tests, which provided qualitatively the same answers, reinforcing the robustness of the results. Because there is no qualitative difference, but these repeated-measure tests do necessitate excluding some individuals, we report the results of the between-group comparisons to best reflect the full dataset. (iii) We measured the aggregate effect of hearing a playback treatment on feeding time by calculating the total time a puma was observed feeding during each treatment over the course of 24 h. We Box-Cox transformed these data to meet normality assumptions and tested for differences using ANOVA. Again, because some pumas were exposed to both treatments, we began by including individual identity as a random effect in the feeding analysis (the only parametric test), but because this did not explain any additional variation we removed it from the model and accordingly report results from the univariate (predator versus non-predator) fixed effects model.

3. Results

We successfully conducted 29 experimental trials on 17 pumas. All 17 heard non-predator (frog) playbacks and 12 were exposed to both predator (human) and non-predator (frog) playbacks. Pumas fled in the majority of cases (83%) upon first hearing humans and only once upon first hearing frogs (6%; figure 1a; Fisher's exact $p < 0.001$). The latency to return time after pumas first heard a treatment was significantly greater in response to human playbacks (figure 1b; M-W $U_{12,17} = 151.5$, $p = 0.028$) because pumas returned to the carcass less often following their first hearing of a human playback (42% of trials) than following their first hearing of a non-predator (frog) playback (18%), or if they did return, they took longer to do so after first hearing humans

(median = 20 min, range = 0–257) than after first hearing frogs (median = 2 min, range = 0–40). Feeding time was significantly less for the human treatment than the non-predator (frog) treatment ($F_{1,27} = 5.74$, $p = 0.024$; figure 1c). Over the course of 24 h, pumas fed for less than half as long when exposed to humans (4.6 ± 2.9 SE min; median = 0.03 min) as when exposed to frogs (10.4 ± 3.1 SE min; median = 4.5 min).

4. Discussion

Our results experimentally demonstrate that fear of the human 'super predator' induces substantial behavioural changes in pumas, ultimately leading to significant reductions in time spent feeding. We observed almost unanimous fleeing behaviour in response to the human playback treatment, directly tying a strong fear response to subsequent declines in feeding. Our previous work showed that pumas nearly halve their feeding time of deer in suburban areas compared to areas with less housing [5]. The halving of feeding time during human trials compared to non-predator trials that we observed in this study suggests that this difference in puma behaviour at kills based on nearby housing densities can be fully accounted for by fear, and that this consequently causes pumas to increase their kill rates by 36% [5]. In a previous study we found that deer occupancy was not influenced by housing density, therefore it is unlikely that relative deer availability explains observed changes in kill rate [18]. Our results support the conclusion that increased kill rates in residential areas are driven by a top-down mechanism (fear of humans), rather than a bottom-up mechanism (availability of prey). Thus, non-consumptive forms of human disturbance may alter the ecological role of large carnivores by affecting the link between these top predators and their prey.

Prey generally respond to both direct (e.g. predator vocalizations) and indirect (e.g. moonlight or cover) cues of predation risk, and the strength of their response depends upon both the nature and number of cues. A single direct cue typically induces a stronger response than a single indirect cue, but multiple indirect cues may induce an equivalent or even stronger response than a single direct one [24–26]. Our experiment demonstrates that pumas respond fearfully to a direct cue indicative of the immediate presence of the human 'super predator' (i.e. hearing

human vocalizations). In human-dominated landscapes, pumas are exposed to multiple indirect cues indicative of the presence of the human 'super predator' (e.g. anthropogenic lighting, sounds of vehicles and dogs), and our previous work shows that pumas respond to these indirect cues [5,6,18]. Our purpose in testing the responses of pumas to human vocalizations was to evaluate the perception of humans as predator, as explained above. In the present study, exposure to a single direct cue (hearing human vocalizations) had the same magnitude of effect on feeding time as did cumulative indirect (e.g. lighting, vehicles) and less direct (e.g. hearing humans at a distance) cues [5], as might be expected in the response of any prey to any predator. Fear-induced trophic cascades are not caused by responses to a specific cue, but by prey responding to any and every cue signalling the presence of the predator it fears [9,10,25].

Our results are consistent with theoretical predictions made from other playback experiments that have demonstrated the ability for humans to cause fear responses in wildlife [3] and for fear responses in carnivores to cascade to lower trophic levels [10]. We have combined these concepts in context of large carnivores due to their important regulatory role and susceptibility to disproportionately high mortality rates via the human 'super predator' [1]. Our results show that large carnivores are not exempt from human-induced fear, and that human impacts on their feeding behaviour might have surprising cascading effects.

In this study, we implemented a novel ABR playback experiment [21] to quantify a large carnivore's behavioural response to humans. Such direct testing of human disturbance has not previously been done on a large carnivore due to the challenge of observing these animals in the wild. Our use of recent puma kill sites accompanied by the integrated ABR technology allowed us to make inferences on humans as a driver of risk–foraging trade-offs in a large carnivore.

Similar methods could be executed on other elusive species to investigate a diversity of risk responses to invasive predators, extirpated predators or competing predators.

Overlap between large carnivores and humans is increasing in regions where continued agricultural and residential development coincides with the recovery of large carnivore populations [27,28]. Although the coadaptation of humans and carnivores can lead to coexistence in human-dominated landscapes [29], carnivore behavioural adaptations might result in unintended indirect effects on other species [11]. Our work suggests that fear-induced trophic cascades instigated by the human 'super predator' are likely to contribute to altered ecological dynamics in human-dominated landscapes. As the habitats used by wildlife and humans are increasingly shared, additional work is needed on the extent to which fear in top predators cascades through ecosystems.

Data accessibility. Data have been made available in the Dryad data repository: <http://dx.doi.org/10.5061/dryad.6pn0b> [30].

Authors' contributions. J.A.S., M.C., C.C.W. and L.Y.Z. conceived of; J.A.S., J.P.S., M.C., C.C.W. and L.Y.Z. designed; and J.A.S., A.C. and C.C.W. conducted the study. J.A.S., M.C., A.C. and D.R. processed and analysed data. J.A.S. wrote the manuscript, with help from J.P.S., M.C., L.Y.Z. and C.C.W. All authors gave final approval for publication.

Competing interests. We have no competing interests.

Funding. Funding was provided by National Science Foundation grant #1255913, the Gordon and Betty Moore Foundation, and the Natural Sciences and Engineering Research Council of Canada.

Acknowledgements. We thank P. Houghtaling, C. Fust, S. McCain and many undergraduate volunteers for assistance with fieldwork. We thank the California Department of Fish and Wildlife, C. Wylie, D. Tichenor, B. Milsap and T. Collinsworth for their assistance capturing pumas, and the many landowners that have allowed us access to their property. We thank Rob Magrath for his helpful comments on the manuscript.

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