

10-1-2019

Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice

Justin P. Suraci
University of California, Santa Cruz

Michael Clinchy
The University of Western Ontario

Liana Y. Zanette
The University of Western Ontario, lzanette@uwo.ca

Christopher C. Wilmers
University of California, Santa Cruz

Follow this and additional works at: <https://ir.lib.uwo.ca/biologypub>



Part of the [Biology Commons](#)

Citation of this paper:

Suraci, Justin P.; Clinchy, Michael; Zanette, Liana Y.; and Wilmers, Christopher C., "Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice" (2019). *Biology Publications*. 120.
<https://ir.lib.uwo.ca/biologypub/120>

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28

DR. JUSTIN SURACI (Orcid ID : 0000-0001-5952-2186)

Article type : Letters

LETTER

Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice

Justin P. Suraci¹, Michael Clinchy², Liana Y. Zanette², Christopher C. Wilmers¹

¹Center for Integrated Spatial Research, Environmental Studies Department, University of California, Santa Cruz, CA 95064, USA

² Department of Biology, Western University, London, ON N6A 5B7, Canada

Author email addresses: justin.suraci@gmail.com; mclinchy@uwo.ca; lzanette@uwo.ca; cwilmers@ucsc.edu

Corresponding author:

Justin Suraci

Environmental Studies Department, University of California, 1156 High Street, Santa Cruz, CA, 95064

Phone: 831-999-0492

Running title: Fear of humans has landscape-scale impacts

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/ELE.13344](https://doi.org/10.1111/ELE.13344)

This article is protected by copyright. All rights reserved

29 **Keywords:** ecology of fear, human impacts, landscape of fear, large-scale field manipulation,
30 playback experiment

31
32 **Authorship:** All authors conceived of and designed the study. JPS led the fieldwork and analysis
33 with support from CCW. JPS drafted the manuscript and all authors provided valuable feedback
34 on the paper.

35
36 **Data accessibility:** All data used in the analyses presented here are available on figshare.
37 <https://doi.org/10.6084/m9.figshare.8315417.v1>

38
39 **Word Counts**

40 Abstract: 147

41 Main text: 4,975

42
43 **Number of references:** 62

44
45 **Number of figures:** 2

46
47 **Abstract**

48 Apex predators such as large carnivores can have cascading, landscape-scale impacts across
49 wildlife communities, which could result largely from the fear they inspire, though this has yet to
50 be experimentally demonstrated. Humans have supplanted large carnivores as apex predators in
51 many systems, and similarly pervasive impacts may now result from fear of the human “super
52 predator”. We conducted a landscape-scale playback experiment demonstrating that the sound of
53 humans speaking generates a landscape of fear with pervasive effects across wildlife
54 communities. Large carnivores avoided human voices and moved more cautiously when hearing
55 humans, while medium-sized carnivores became more elusive and reduced foraging. Small
56 mammals evidently benefited, increasing habitat use and foraging. Thus, just the sound of a
57 predator can have landscape-scale effects at multiple trophic levels. Our results indicate that
58 many of the globally-observed impacts on wildlife attributed to anthropogenic activity may be
59 explained by fear of humans.

60

61 **Introduction**

62 The fear of predators can itself be powerful enough to drive demographic and community-level
63 changes in wildlife systems, as demonstrated in a growing number of recent experiments
64 (Zanette *et al.* 2011; LaManna & Martin 2016; Suraci *et al.* 2016). The impacts of fear are
65 typically mediated by changes in prey behavior (Schmitz *et al.* 1997; Brown & Kotler 2004),
66 which may vary spatially with changes in the prey's perception of predation risk across the
67 landscape (Gaynor *et al.* 2019). Anthropogenic activity is reshaping wildlife behavior across
68 human-dominated landscapes, disrupting movement (Tucker *et al.* 2018), forcing shifts to
69 nocturnality (Gaynor *et al.* 2018), and changing the way predators interact with their prey (Smith
70 *et al.* 2015). Humans are themselves major predators (Darimont *et al.* 2009), killing some
71 species, particularly large and medium-sized carnivores, at many times the rate at which they are
72 killed by non-human predators (Darimont *et al.* 2015), and fear of the human “super predator”
73 (Darimont *et al.* 2015) may therefore be a significant driver of observed changes in wildlife
74 behavior (Oriol-Cotterill *et al.* 2015; Suraci *et al.* 2019). Given that humans have evidently
75 superseded large carnivores as apex predators in many ecosystems (Ordiz *et al.* 2013a; Oriol-
76 Cotterill *et al.* 2015; Kuijper *et al.* 2016), our mere presence may be expected to generate
77 landscapes of fear (Gaynor *et al.* 2019) with spatial extents and breadth of trophic impacts equal
78 to or greater than those presently attributed to large carnivores (Laundré *et al.* 2001; Palmer *et al.*
79 2017). Yet whether fear of the human “super predator”, or indeed any large apex predator,
80 generates landscapes of fear with impacts across wildlife communities remains to be tested
81 experimentally.

82 A large number of correlative studies suggest that some wildlife species respond fearfully
83 to human activity (Fernandez-Juricic *et al.* 2005; Stankowich & Blumstein 2005; Bateman &
84 Fleming 2017), but whether such responses are driven by perceived risk from humans as
85 predators or by a generalized response to “disturbance” (e.g., sudden noises, looming objects) is
86 often unclear (Frid & Dill 2002; Stankowich 2008). Experimentally testing predator-specific
87 responses requires manipulating something the prey is likely to perceive as being specific to that
88 predator (e.g., vocalizations, odors) in conjunction with a non-predator-specific control for the
89 generalized disturbance potentially caused by manipulations. Recently, small-scale (≤ 50 m),
90 short-term (≤ 2 h) controlled experiments on single prey species have demonstrated that wildlife

91 regularly killed by humans exhibit strong fear responses to human vocalizations, just as prey
92 respond fearfully to the vocalizations of any other predator (Hettena *et al.* 2014; McComb *et al.*
93 2014; Clinchy *et al.* 2016; Smith *et al.* 2017). By isolating human predator-specific responses,
94 such experiments differentiate the impacts of fear of humans as predators from the myriad other
95 aspects of the anthropogenic environment likely to affect wildlife behavior (e.g., enhanced food
96 resources, habitat fragmentation (Bateman & Fleming 2012; Newsome *et al.* 2015; Tucker *et al.*
97 2018)). By scaling up such experiments we can thus quantify how the fear of humans as
98 predators impacts wildlife at the landscape and community levels.

99 To experimentally test whether the magnitude of effects caused by fear of an apex
100 predator (in this case humans) can extend to having landscape-scale impacts across wildlife
101 communities, we conducted spatially replicated, landscape-scale manipulations of perceived
102 human presence. We sequentially broadcast playbacks of people talking or control sounds for
103 five weeks (followed by the opposite treatment for a subsequent five weeks) over spatial scales
104 (1 km²) comparable to those of the largest mammalian predator exclusion experiments (Salo *et al.*
105 2010), and simultaneously quantified the responses of multiple mammal species across three
106 trophic levels. The study was conducted in the Santa Cruz Mountains of central California. Like
107 an increasingly large proportion of the planet (Venter *et al.* 2016), this region consists of wildlife
108 habitat in close proximity to urban and suburban development, and is thus heavily used by
109 people (Wang *et al.* 2015). The Santa Cruz Mountains support a single native large carnivore,
110 the mountain lion (*Puma concolor*), and several smaller predators (for brevity, referred to as
111 “medium-sized carnivores”) including bobcats (*Lynx rufus*), striped skunks (*Mephitis mephitis*),
112 and Virginia opossums (*Didelphis virginiana*), all of which have been shown to alter their
113 behavior in response to the gradient of human development that exists across the region
114 (Wilmers *et al.* 2013; Wang *et al.* 2015). Small-scale experiments replicated across this region
115 previously demonstrated that mountain lions here exhibit strong fear responses to hearing human
116 voices, fleeing food caches, and feeding less as a consequence (Smith *et al.* 2017). Medium-
117 sized carnivores similarly exhibited fear-induced reductions in feeding and shifts in temporal
118 activity in response to the small-scale experimental presentation of human voices (Clinchy *et al.*
119 2016). As is true for large and medium-sized carnivores globally (Ordiz *et al.* 2013a; Darimont
120 *et al.* 2015), humans are a major source of mortality for mountain lions in our study area, with
121 legal and illegal shooting accounting for 59.1% of known-cause mortalities of collared animals

122 since 2008 (C. Wilmers, *unpublished data*). Bobcats, skunks, and opossums are all common
123 targets of predator control (Conner & Morris 2015), and are all legally hunted in California, with
124 no legal limits on killing skunks and opossums (California Department of Fish and Wildlife
125 2018). Correlational results from our study area indicate that bobcats are sensitive to risk from
126 humans, decreasing diurnal activity in areas of high human development, but suggest that skunks
127 and opossums may prefer more developed areas (Wang *et al.* 2015). Medium-sized carnivores
128 such as skunks and opossums often rely heavily on human subsidies, including food waste
129 (Bateman & Fleming 2012), and thus could be forced to balance the risk of anthropogenic
130 mortality against the benefits of living near humans.

131 Given the evidence that carnivores fear humans as predators, both in our study area and
132 in general, our objective was to experimentally test whether such fear leads to landscape-scale
133 impacts across wildlife communities. We quantified the large-scale effects of fear of humans as
134 predators on carnivore movement, activity, and foraging behavior using GPS collars (mountain
135 lions) and camera traps (bobcats, skunks, and opossums). Correlational studies suggest that fear-
136 induced suppression of carnivore behavior by apex predators may cascade to benefit small
137 mammal prey (Brook *et al.* 2012; Gordon *et al.* 2015), though this has yet to be shown
138 experimentally. We therefore additionally tested whether the fear that humans induce in
139 carnivores can have cascading effects on the behavior of lower trophic level animals, using live-
140 trapping and provisioned food patches to document effects on habitat use and foraging by small
141 mammals (deer mice *Peromyscus* spp. and woodrats *Neotoma fuscipes*) known to be preyed
142 upon by several of the carnivores in our study (Azevedo *et al.* 2006; Smith *et al.* 2018).

143 In a major reclarification of the landscape of fear concept, Gaynor *et al.* (2019) define it
144 as spatial variation in the prey's perception of predation risk, influenced by, but distinct from,
145 both the physical landscape and actual risk of mortality from predators. Here we use the
146 sequential presentation of human and control vocalizations at each of our 1-km² sites to
147 manipulate the perception of predation risk across the same physical landscapes, thus keeping
148 physical characteristics and actual mortality risk constant. We thereby experimentally
149 demonstrate that a landscape of fear, resulting solely from variation in the perception of risk
150 from an apex predator, can have pervasive effects across wildlife communities. That such effects
151 can result from the fear of humans as predators indicates that this may be an important factor

152 underlying many of the globally-observed changes in wildlife behaviour associated with
153 anthropogenic activity (Gaynor *et al.* 2018; Tucker *et al.* 2018).

154

155 **Methods**

156 **Study area.** The study was conducted at two 1-km² experimental sites (SA and SVR), separated
157 by 26 km (Fig. S1). Both sites were closed to public access, and human presence was therefore
158 low relative to elsewhere in the Santa Cruz Mountains. The presence of humans (including
159 researchers) and vehicles did not differ between experimental sites during the study (Mann-
160 Whitney U-test comparing occurrences per camera night on n = 12 cameras per site; humans: $p =$
161 0.643; vehicles: $p = 0.655$). Work was conducted between 29 May and 31 August 2017.

162 For additional details on the study area and species, see Appendix S1. All procedures
163 described below were approved by the Institutional Animal Care and Use Committee of the
164 University of California, Santa Cruz (Protocol WilmC1612) and the California Department of
165 Fish and Wildlife (Permits SC-11968 and SC-12383).

166

167 **Playbacks and study design.** We manipulated the perceived presence of humans on the
168 landscape using playbacks of human and control vocalizations broadcast sequentially for five
169 weeks each at both 1-km² experimental sites. Following established protocols (Suraci *et al.*
170 2016; Smith *et al.* 2017), we compared wildlife responses to human vocalizations with responses
171 to Pacific treefrog (*Pseudacris regilla*) vocalizations. Tree frogs, like humans, can be heard both
172 day and night in our study area, but unlike humans, their perceived presence should be
173 completely benign given that treefrogs are unlikely to be predators, competitors, or prey of any
174 study species. As discussed in detail in Appendix S1 (Supplementary Methods – Playback
175 Treatments), there is ample evidence to suggest that wildlife in the Santa Cruz Mountains will be
176 familiar with both human and tree frog vocalizations.

177 Playbacks were broadcast from 25 speakers arranged in a 5 x 5 grid at each experimental
178 site (Fig. S1). Each speaker played a randomized playlist of human or frog recordings (n = 10
179 exemplars of each) interspersed by silence such that each individual speaker was broadcasting
180 40% of the time and silent 60% of the time. Speakers were thus continuously active, but
181 presentation of cues was random and sporadic across the playback grid. The human treatment
182 thereby mimicked a wildland-urban interface in that human vocalizations were relatively

183 infrequent, but from any location within the playback grid, a human could occasionally be heard
184 at any time. All playbacks were broadcast at a standardized volume of ~ 80 dB at 1 m (human =
185 $78.7 \text{ dB} \pm 1.9 \text{ SD}$; frog = $79.2 \text{ dB} \pm 2.4$). Additional details of the playback treatments are
186 provided in Appendix S1.

187 We employed a repeated-measures design with each experimental site receiving either
188 the human or control treatment for five weeks (treatment period 1), followed by the opposite
189 treatment for a subsequent five weeks (treatment period 2) with eight days of silence between the
190 two treatment periods. Thus, both experimental sites received each treatment in opposite order,
191 and as such, detecting consistent responses to playback treatments across sites is critical to
192 concluding that treatments had a significant effect. We therefore included a test for treatment x
193 site interaction in all analyses presented below and only concluded that treatments drove
194 observed changes when no significant interaction was detected (see Tables S1-S8). We also
195 present visualizations of site-level data for all analyses (Figures S2-S7) to illustrate the
196 consistency of treatment effects across sites.

197
198 **Monitoring mountain lion responses to playbacks.** We monitored the responses of seven
199 mountain lions (four females, three males) whose home ranges overlapped one of our two
200 experimental sites. Five individuals (four females, one male) used SVR, while two males used
201 SA. Mountain lions were captured using trailing hounds or cage traps and fitted with GPS
202 collars (GPS Plus, Vectronics Aerospace, Berlin, Germany) with a 5-min fix interval.

203 We focused mountain lion movement analyses on only those periods when an individual
204 was within audible range of a playback grid (termed an “encounter” with the playbacks) and
205 used a repeated-measures design to compare responses of individual mountain lions to both
206 playback treatments (Fig. 1). We considered the audible range of the speakers to extend 200m
207 out from the speaker grid itself (see Appendix S1), and also ran all analyses using a smaller
208 buffer size (150m), which yielded similar results. Five mountain lions encountered the
209 playbacks on multiple occasions, with subsequent encounters separated by 19.1 days on average
210 (range = 4.6 to 38.6 days). Median number of encounters per individual was 2 (range = 1 to 5;
211 total encounters across all individuals = 17).

212 For all mountain lion GPS locations taken within the 200m audible range, we determined
213 the distance to the nearest playback speaker and the animal’s movement speed. For each

214 encounter, we then calculated average distance to the nearest speaker (an estimate of speaker
215 avoidance) and average movement speed across all locations for that encounter. We took the
216 inverse of movement speed as an estimate of “cautiousness”, moving more slowly being
217 considered greater cautiousness. We tested for effects of playback treatment, experimental site,
218 and a treatment x site interaction on avoidance and cautiousness using linear mixed-effects
219 models (LMM), with mountain lion ID as a random effect. Cautiousness (movement speed⁻¹)
220 was log-transformed to meet normality assumptions. Unless otherwise noted, we confirmed
221 adequate fit of these and all other frequentist models through visual inspection of residuals and
222 assessed significance of model terms using Type II Wald’s chi-squared tests (Table S1). Finally,
223 we confirmed that observed changes in medium-sized carnivore behavior between treatments
224 (see below) were not due to changes mountain lion presence by testing for differences in time
225 spent by mountain lions near experimental sites (see Appendix S1 and Table S1 for details).

226

227 **Medium-sized carnivore responses to playbacks.** At each experimental site, we deployed a
228 grid of 12 camera traps, which ran continuously throughout the experiment (camera deployment
229 details in Appendix S1). We scored camera trap images for the presence of three medium-sized
230 carnivore species that occurred at both experimental sites, which prior correlational research in
231 the region indicates are affected by human development (Wang *et al.* 2015): bobcats, striped
232 skunks, and Virginia opossums. We considered images of the same species on the same camera
233 to be separate detections if they were separated by > 30 min (Wang *et al.* 2015; Suraci *et al.*
234 2017). Two other medium-sized carnivore species (raccoons *Procyon lotor* and gray foxes
235 *Urocyon cinereoargenteus*) occasionally occurred on camera traps, but were detected too
236 infrequently to permit statistical analyses, raccoons only occurring on three cameras at one site
237 and foxes only during a subset of treatment periods.

238

239 *Bobcat temporal activity*

240 Prior research (Wang *et al.* 2015) shows that, whereas bobcats are diurnally active 29.6% of the
241 time, skunks and opossums are almost exclusively nocturnal (94% and 96.6% nocturnality
242 respectively). We therefore tested whether playback treatments affected temporal activity for
243 bobcats, the only species with sufficient diurnal activity to expect an effect. We calculated the
244 overlap between temporal activity during control and human treatments using the kernel density

245 estimation procedure described by Ridout and Linkie (Ridout & Linkie 2009; Linkie & Ridout
246 2011). We estimated probability density distributions for bobcat occurrences on camera across
247 the 24-hr day separately for the control and human treatment periods. We then calculated the
248 coefficient of overlap ($\hat{\Delta}$, range 0 to 1) between these two activity distributions (Ridout & Linkie
249 2009), along with 95% CIs (via 10,000 bootstrap replicates (Linkie & Ridout 2011)) using the
250 overlap package in R (Meredith & Ridout 2014). We calculated overlap separately for each
251 experimental site and then with data from both sites pooled. We considered there to be evidence
252 of a change in temporal activity if overlap in activity distributions during control and human
253 treatment was < 0.90 .

254 Bobcats exhibited a consistent shift in temporal overlap between human and control
255 treatments across both experimental sites (Table S2). We therefore quantified the degree to
256 which this temporal shift constituted a reduction in diurnal activity in favor of nocturnality
257 during the human treatment. For each bobcat detection on camera ($n = 44$ on 12 cameras) we
258 calculated the absolute value of the difference (in hours) between the timestamp of the detection
259 and the middle of the night (the midpoint between sunset and sunrise, averaged across the study
260 period; 01:15) such that detections near midday received the highest values of this diurnal
261 activity metric. We tested for the effects of playback treatment, experimental site, and a
262 treatment \times site interaction on diurnal activity using LMM with camera site as a random effect.

263
264 *Modeling medium-sized carnivore occupancy and detection frequency at camera sites*
265 To test whether fear of humans affected medium-sized carnivore behavior at the landscape scale,
266 we developed a hierarchical model describing (i) use by a given species of individual camera
267 sites within each experimental site, and (ii) frequency of detections of that species at used camera
268 sites, a proxy for activity level. We based our model on multi-species occupancy models
269 (Burton *et al.* 2012; Broms *et al.* 2016), but with two distinctions: (i) we consider camera site use
270 (rather than occupancy *per se*), as individual carnivores could use more than one camera site, and
271 (ii) we modeled the frequency of detections of a given species at a camera site (a Poisson
272 process), rather than the binary estimate of detected/not detected typically used in occupancy
273 models. We treated each week of the experiment as a survey period (Wang *et al.* 2015; Moll *et*
274 *al.* 2018), yielding five replicate surveys per treatment at each camera site. Three data points
275 were excluded from the analysis when cameras failed to record data for the full week. We

276 formulated our analysis as a zero-inflated negative binomial model (Moll *et al.* 2018), allowing
277 occupancy at a camera site (binomial submodel) to vary between playback treatments, and
278 explicitly modeling detection frequency (negative binomial submodel) as a function of
279 experimental site, playback treatment, and their interaction. We analyzed the hierarchical
280 detection frequency model in a Bayesian framework using the JAGS language (Plummer 2003)
281 via the R2jags package (Su & Yajima 2015) in R. For a full model description and details on the
282 Bayesian analysis (including JAGS code and model fit), see Appendices S1 and S2. Model
283 results are present in Tables S3 and S4.

284 The above model indicated a substantial reduction in skunk detection frequency during
285 the human treatment at both sites. To confirm the robustness of this result, we performed a
286 simplified version of the analysis, using a Wilcoxon matched-pairs test to compare total skunk
287 detections during the human and control treatments on each camera.

288

289 *Medium-sized carnivore foraging trials*

290 We created feeding patches (consisting of a single boiled chicken egg) at each of the 12 camera
291 locations within each experimental site. We estimated patch discovery rate (i.e., days required
292 for a medium-sized carnivore to find and consume the egg, determined from camera trap images)
293 as an index of carnivore foraging efficiency. Eggs were set out twice during each treatment
294 period (during weeks 2 and 4), yielding a total of 96 trials. To standardize availability, we
295 consider only those trials in which a medium-sized carnivore ultimately discovered the patch (n
296 = 36), as some eggs were taken by other species (e.g., corvids) before being discovered by
297 carnivores. Discovery rate data were log-transformed to satisfy normality assumptions and fit by
298 LMM, using camera site as a random effect. We tested for effects of treatment, experimental
299 site, species, and session (first or second deployment during each treatment), and treatment x site
300 interaction. Opossums made the majority of foraging patch discoveries ($n = 20$) and skunks
301 made the remainder ($n = 16$), with no discoveries made by bobcats. We first analyzed data from
302 opossums and skunks combined, and then fit species-specific models, using the model terms just
303 mentioned with the exception of species (Table S5).

304

305 **Deer mouse spatial capture-recapture.** We conducted a spatial capture-recapture study using
306 four grids of live traps at each experimental site. Grids were trapped immediately prior to the

307 start of any playbacks, and immediately following each playback treatment period. All captured
308 mice were marked with unique ear tags. See Appendix S1 and Fig. S1 for live trapping details.
309 We analyzed live trapping data using spatial capture-recapture (SCR) models (Royle *et al.* 2013),
310 which permit quantification of the amount of space used by individual animals (σ in SCR
311 models; Appendix S1 and (Royle *et al.* 2013)). We modeled spatially explicit capture histories
312 using a zero-inflated binomial model with data augmentation (Royle & Dorazio 2008; Royle *et*
313 *al.* 2013). Detection probability and/or space use could be affected by playback treatment if
314 mice alter their movements in response to treatment-induced changes in carnivore behaviour.
315 We estimated the effect of playback treatment on detection probability and space use by
316 calculating averages of these parameters (across all trapping grids) for trapping sessions
317 following the control and human treatments. Treatment-level averages were then subtracted to
318 estimate the average difference in parameter values between control and human treatments. If
319 the 95% credible intervals (CrI) of the difference between treatments did not cross zero, we
320 considered there to be evidence of a treatment effect on the parameter of interest (Table S6).
321 Average values (\pm 95% CrI) of the space use parameter (σ) during each treatment were used to
322 calculate the average area of habitat used during each treatment, following the procedure
323 outlined by Royle *et al.* (2013, pg. 136). For a full description of the deer mouse SCR model and
324 the Bayesian analysis of this model, see Appendices S1 and S2. Model results are presented in
325 Tables S6 and S7.

326

327 **Small mammal foraging trials.** Two small mammal foraging patches, separated by < 3m, were
328 deployed at each of the 12 camera locations within each experimental site, one under protective
329 cover (shrubs) and one in the open. Each patch consisted of an aluminum tray filled with 10g of
330 millet seed mixed into 1l of sifted sand. Patches thus required time to exploit, allowing time for
331 the accumulation of camera trap images and/or small mammal droppings in trays. Patches were
332 deployed twice during each 5-week treatment period (during weeks 2 and 4) and were left in
333 place for two consecutive nights, with millet and sand refreshed after the first night. We focus
334 our analyses on the proportion of available patches visited on a given night and include only
335 those trials in which visitation or lack thereof by small mammals (deer mice or woodrats) could
336 be determined with high confidence based on the presence or absence of camera trap images
337 and/or droppings (n = 256). Preliminary analysis indicated that open patches were largely

338 avoided overall (Appendix S1, Table S8). We therefore restricted our analysis to patches under
339 cover.

340 We coded whether a particular patch was visited (1) or not (0), and analyzed these data
341 using a generalized LMM with binomial error distribution, including camera site as a random
342 effect. We tested for effects of treatment, experimental site, night (first or second night of patch
343 deployment), moon illuminance, and a treatment x experimental site interaction. Adequate
344 model fit was assessed through inspection of scaled residuals using the DHARMA R package
345 (Harting 2018).

346

347 **Results**

348 Fear of humans drove significant changes in how mountain lions moved through the same
349 physical landscape (Fig. 1). Mountain lions avoided areas of perceived human presence,
350 encountering the playback grids 30% less often when human sounds were broadcast, and
351 maintaining a 29% greater distance to the nearest speaker during human playbacks relative to
352 controls (Figs. 2a and S2; LMM: Wald's $\chi^2_1 = 6.33$, $P = 0.012$). Mountain lions also moved
353 more cautiously when hearing human playbacks, reducing average movement speed by 34%
354 (Figs. 2a and S2; LMM: Wald's $\chi^2_1 = 4.66$, $P = 0.031$).

355 Fear of humans had an overall suppressive effect on medium-sized carnivore behavior
356 (Fig. 2B). Bobcats reduced diurnal activity by 31% when hearing humans (Figs. 2b and S3;
357 Table S2; LMM: Wald's $\chi^2_1 = 4.71$, $P = 0.030$), shifting their diel activity patterns towards
358 increased nocturnality (overlap ($\hat{\Delta}$) in activity between treatment and control = 0.68 (95% CI:
359 0.48-0.86); Fig. S8). Skunks were the only species to exhibit a reduction in overall activity
360 (Table S4), reducing activity levels by 40% during the human treatment (Figs. 2b and S4;
361 detection frequency model: treatment coefficient = -1.12 (95% credible interval: -2.37 to -0.04)),
362 and were therefore detected less frequently on camera traps (Wilcoxon test, $P = 0.007$; $n = 24$).
363 When considering all trials in which a medium-sized carnivore discovered a provisioned food
364 patch, fear of humans had a significant negative effect on food patch discovery rate (Table S5;
365 LMM: Wald's $\chi^2_1 = 5.88$, $P = 0.015$). Species specific models indicated that this effect was
366 largely driven by opossums. The sound of humans led to a 66% reduction in opossum foraging
367 efficiency (Figs. 2b and S5; Table S5; LMM: Wald's $\chi^2_1 = 8.77$, $P = 0.003$) such that opossums
368 took on average 1.8 days longer to discover food patches during the human treatment.

369 Small mammals benefitted from the apparent presence of humans, increasing both the
370 amount of habitat and number of foraging opportunities exploited. During the human treatment,
371 deer mice expanded their space use by 45% relative to controls (Figs. 2c and S6), increasing
372 average area used by 649 m² (95% credible interval = 116 – 1209 m²) while maintaining an
373 overall consistent detection probability across treatments (Tables S6 and S7). Mice and
374 woodrats increased foraging intensity by 17% during the human treatment (Fig. 2c, Table S8;
375 GLMM: Wald's $\chi^2_1 = 4.71$, $P = 0.030$), visiting a significantly higher proportion of provisioned
376 food patches (Figs. S7 and S9).

377

378 **Discussion**

379 Our results experimentally demonstrate that fear of humans as predators can have pervasive
380 impacts across wildlife communities, suppressing movement and activity of large and medium-
381 sized carnivores, with cascading benefits for small mammals (Fig. 2d and e). Thus, spatial
382 variation in the perception of risk from an apex predator can itself create a landscape of fear
383 (Gaynor *et al.* 2019), manifesting in widespread changes in wildlife behavior.

384 Mountain lions significantly altered their movement through the same physical landscape
385 in response to hearing humans (Fig. 1), exhibiting antipredator behaviors comparable to those
386 previously documented in small-scale experiments (Smith *et al.* 2017), but at a substantially
387 larger scale (Fig. 2a). Observational and manipulative studies have similarly found that risk
388 from humans affects large carnivore behavior across the landscape (Valeix *et al.* 2012; Ordiz *et*
389 *al.* 2013b, 2019; Oriol-Cotterill *et al.* 2015; Suraci *et al.* 2019), including in our study area,
390 where increased human development is correlated with impacts on mountain lion movement and
391 habitat use (Wilmers *et al.* 2013; Wang *et al.* 2017). Our results confirm that, even in the
392 absence of changes in human infrastructure (e.g. buildings, roads) or habitat fragmentation,
393 increased human presence can impact large carnivore movement by inducing antipredator
394 responses, which, if sustained for long periods, could lead to effective habitat loss for carnivores
395 by limiting hunting and feeding behavior (Smith *et al.* 2015) or forcing individuals to abandon
396 high risk areas of their home range (Schuette *et al.* 2013).

397 Fear of humans had suppressive effects on medium-sized carnivore activity across all
398 three study species (Fig. 2b), yet as expected from the diversity of carnivore behaviors, their
399 exact responses differed. Our experimental results confirm previous correlational findings

400 (Wang *et al.* 2015) that bobcats become more nocturnal in response to human presence,
401 demonstrating that fear of humans may contribute to the documented global pattern of increased
402 wildlife nocturnality in disturbed habitats (Gaynor *et al.* 2018). Fear of humans also impacts
403 skunks and opossums, causing reductions in overall activity or foraging behavior by these often
404 human-associated species. These results highlight the trade-off such species face between the
405 potential benefits of living in an anthropogenic environment (e.g., abundant food subsidies
406 (Bateman & Fleming 2012; Newsome *et al.* 2015)) and the fear-induced costs of sharing habitat
407 with humans (Fig. 2b). Interestingly, none of the three medium-sized carnivores exhibited
408 changes in overall habitat use between treatments (number of camera sites used; Tables S3),
409 potentially reflecting a limited capacity to do so, at least for species (i.e., skunks and opossums)
410 whose relatively small home ranges likely overlapped substantially with our experimental sites
411 (Appendix S1).

412 Finally, significant increases in small mammal space use and foraging documented
413 during the human playback treatment (Fig. 2c) experimentally demonstrate that the suppression
414 of carnivore behaviour induced by fear of an apex predator (in this case, humans) can have
415 cascading effects on small mammal prey (Brook *et al.* 2012; Gordon *et al.* 2015). These
416 cascading behavioral changes suggest that the presence of people may in some cases act as a
417 “human shield” (Berger 2007) for small mammals, reducing their perceived risk of predation
418 from carnivores. Human shield effects have been suggested to occur in some large carnivore-
419 ungulate systems, with ungulates preferring areas of high human activity because these areas are
420 avoided by carnivores (Hebblewhite *et al.* 2005; Berger 2007; Muhly *et al.* 2011). If similar
421 human shield effects for small mammals are common where human activity is high, this could
422 ultimately lead to increased small mammal abundance in wildlife areas frequented by people, a
423 potentially undesirable consequence of ecotourism (Geffroy *et al.* 2015).

424 Our work provides strong evidence that many of the globally-observed changes in
425 wildlife behavior stemming from anthropogenic activity, including changes in large carnivore
426 habitat use (Valeix *et al.* 2012), broader disruptions of animal movement (Tucker *et al.* 2018),
427 and increased nocturnality (Gaynor *et al.* 2018), can be explained in part by the fear of humans
428 as predators. Moreover, if fear of humans triggers substantial sublethal effects comparable to
429 those fear itself has been demonstrated to cause in other predator-prey systems (e.g., increased
430 physiological stress (Zanette *et al.* 2014), reduced reproductive success (Zanette *et al.* 2011);

431 Cherry *et al.* 2016)), this may translate to additional widespread but largely unmeasured impacts
432 of humans on wildlife populations. Given the potential for sublethal effects, apparently “human-
433 tolerant” species (e.g., medium-sized carnivores using developed areas) could nonetheless
434 experience substantial costs from chronic exposure to perceived risk from humans (Clinchy *et al.*
435 2016). Pervasive fear of humans may also precipitate widespread community-level changes by
436 disrupting natural predator-prey interactions. Human-induced antipredator behavior could
437 compromise top-down ecosystem regulation by large carnivores (Kuijper *et al.* 2016) and limit
438 medium-sized carnivore suppression of small mammals (Levi *et al.* 2012). Given continued
439 human encroachment into most wildlife habitats (Venter *et al.* 2016), we suggest that the fear we
440 human “super predators” inspire, independently of our numerous other impacts on the natural
441 world, may contribute to widespread restructuring of wildlife communities.

442

443 **Acknowledgements:** We thank A. Crabb, L. Vu, R. King, K. Briner, and P. Houghtaling for
444 help in the field, and several volunteers for field assistance and camera trap image scoring. J.
445 Estes, A. Ordiz, C. Packer, V. Penteriani, M. Power, E. Preisser, T. Williams, and two
446 anonymous reviewers provided valuable feedback on earlier versions of the manuscript.
447 Funding was provided by the Gordon and Betty Moore Foundation, National Science Foundation
448 grant #1255913 to CCW, and a Natural Sciences and Engineering Research Council of Canada
449 Discovery Grant to LYZ.

450

451 **References**

- 452 Azevedo, F.C.C., Lester, V., Gorsuch, W., Larivière, S., Wirsing, A.J. & Murray, D.L. (2006).
453 Dietary breadth and overlap among five sympatric prairie carnivores. *J Zool*, 269, 127–
454 135.
- 455 Bateman, P.W. & Fleming, P.A. (2012). Big city life: carnivores in urban environments. *J Zool*,
456 287, 1–23.
- 457 Bateman, P.W. & Fleming, P.A. (2017). Are negative effects of tourist activities on wildlife
458 over-reported? A review of assessment methods and empirical results. *Biol Conserv*, 211,
459 10–19.
- 460 Berger, J. (2007). Fear, human shields and the redistribution of prey and predators in protected
461 areas. *Biol Lett*, 3, 620–623.

462 Broms, K.M., Hooten, M.B. & Fitzpatrick, R.M. (2016). Model selection and assessment for
463 multi-species occupancy models. *Ecology*, 97, 1759–1770.

464 Brook, L.A., Johnson, C.N. & Ritchie, E.G. (2012). Effects of predator control on behaviour of
465 an apex predator and indirect consequences for mesopredator suppression. *J Appl Ecol*,
466 49, 1278–1286.

467 Brown, J.S. & Kotler, B.P. (2004). Hazardous duty pay and the foraging cost of predation. *Ecol*
468 *Lett*, 7, 999–1014.

469 Burton, A.C., Sam, M.K., Balangtaa, C. & Brashares, J.S. (2012). Hierarchical multi-species
470 modeling of carnivore responses to hunting, habitat and prey in a West African protected
471 area. *PLOS ONE*, 7, e38007.

472 California Department of Fish and Wildlife. (2018). *California Fish and Wildlife Commission*
473 *Mammal Hunting Regulations 2018-2019*. 472.

474 Cherry, M.J., Morgan, K.E., Rutledge, B.T., Conner, L.M. & Warren, R.J. (2016). Can coyote
475 predation risk induce reproduction suppression in white-tailed deer? *Ecosphere*, 7,
476 e01481.

477 Clinchy, M., Zanette, L.Y., Roberts, D., Suraci, J.P., Buesching, C.D., Newman, C., *et al.*
478 (2016). Fear of the human “super predator” far exceeds the fear of large carnivores in a
479 model mesocarnivore. *Behav Ecol*, 27, 1826–1832.

480 Conner, L.M. & Morris, G. (2015). Impacts of mesopredator control on conservation of
481 mesopredators and their prey. *PLoS ONE*, 10, e0137169.

482 Darimont, C.T., Carlson, S.M., Kinnison, M.T., Paquet, P.C., Reimchen, T.E. & Wilmers, C.C.
483 (2009). Human predators outpace other agents of trait change in the wild. *PNAS*, 106,
484 952–954.

485 Darimont, C.T., Fox, C.H., Bryan, H.M. & Reimchen, T.E. (2015). The unique ecology of
486 human predators. *Science*, 349, 858–860.

487 Fernandez-Juricic, E., Venier, M.P., Renison, D. & Blumstein, D.T. (2005). Sensitivity of
488 wildlife to spatial patterns of recreationist behavior: A critical assessment of minimum
489 approaching distances and buffer areas for grassland birds. *Biol Conserv*, 125, 225–235.

490 Frid, A. & Dill, L.M. (2002). Human-caused disturbance stimuli as a form of predation risk.
491 *Conserv Ecol*, 6, 11.

492 Gaynor, K.M., Brown, J.S., Middleton, A.D., Power, M.E. & Brashares, J.S. (2019). Landscapes
493 of Fear: Spatial patterns of risk perception and response. *Trends Ecol Evol*, 34, 355–368.

494 Gaynor, K.M., Hojnowski, C.E., Carter, N.H. & Brashares, J.S. (2018). The influence of human
495 disturbance on wildlife nocturnality. *Science*, 360, 1232–1235.

496 Geffroy, B., Samia, D.S.M., Bessa, E. & Blumstein, D.T. (2015). How Nature-based tourism
497 might increase prey vulnerability to predators. *Trends Ecol & Evol*, 30, 755–765.

498 Gordon, C.E., Feit, A., Grüber, J. & Letnic, M. (2015). Mesopredator suppression by an apex
499 predator alleviates the risk of predation perceived by small prey. *Proc R Soc B*, 282,
500 20142870.

501 Harting, F. (2018). DHARMA: Residual diagnostics for hierarchichal (multi-level/mixed)
502 regression models. *R package version 0.2.0*.

503 Hebblewhite, M., White, C.A., Nietvelt, C.G., McKenzie, J.A., Hurd, T.E., Fryxell, J.M., *et al.*
504 (2005). Human activity mediates a trophic cascade caused by wolves. *Ecology*, 86, 2135–
505 2144.

506 Hettena, A.M., Munoz, N. & Blumstein, D.T. (2014). Prey Responses to Predator’s Sounds: A
507 Review and Empirical Study. *Ethology*, 120, 427–452.

508 Kuijper, D.P.J., Sahlén, E., Elmhagen, B., Chamailié-Jammes, S., Sand, H., Lone, K., *et al.*
509 (2016). Paws without claws? Ecological effects of large carnivores in anthropogenic
510 landscapes. *Proc R Soc B*, 283, 20161625.

511 LaManna, J.A. & Martin, T.E. (2016). Costs of fear: behavioural and life-history responses to
512 risk and their demographic consequences vary across species. *Ecol Lett*, 19, 403–413.

513 Laundré, J.W., Hernández, L. & Altendorf, K.B. (2001). Wolves, elk, and bison: reestablishing
514 the “landscape of fear” in Yellowstone National Park, U.S.A. *Can J Zool*, 79, 1401–1409.

515 Levi, T., Kilpatrick, A.M., Mangel, M. & Wilmers, C.C. (2012). Deer, predators, and the
516 emergence of Lyme disease. *PNAS*, 109, 10942–10947.

517 Linkie, M. & Ridout, M.S. (2011). Assessing tiger–prey interactions in Sumatran rainforests. *J*
518 *Zool*, 284, 224–229.

519 McComb, K., Shannon, G., Sayialel, K.N. & Moss, C. (2014). Elephants can determine ethnicity,
520 gender, and age from acoustic cues in human voices. *PNAS*, 111, 5433–5438.

521 Meredith, M. & Ridout, M. (2014). overlap: Estimates of coefficient of overlapping for animal
522 activity patterns. *R package version 0.3.2*.

- 523 Moll, R.J., Cepek, J.D., Lorch, P.D., Dennis, P.M., Robison, T., Millspaugh, J.J., *et al.* (2018).
524 Humans and urban development mediate the sympatry of competing carnivores. *Urban*
525 *Ecosyst*, 21, 765–778.
- 526 Muhly, T.B., Semeniuk, C., Massolo, A., Hickman, L. & Musiani, M. (2011). Human activity
527 helps prey win the predator-prey space race. *PLOS ONE*, 6, e17050.
- 528 Newsome, T.M., Dellinger, J.A., Pavey, C.R., Ripple, W.J., Shores, C.R., Wirsing, A.J., *et al.*
529 (2015). The ecological effects of providing resource subsidies to predators. *Global Ecol*
530 *Biogeogr*, 24, 1–11.
- 531 Ordiz, A., Bischof, R. & Swenson, J.E. (2013a). Saving large carnivores, but losing the apex
532 predator? *Biol Conserv*, 168, 128–133.
- 533 Ordiz, A., Moen, G.K., Sæbø, S., Stenset, N., Swenson, J.E. & Støen, O.-G. (2019). Habituation,
534 sensitization, or consistent behavioral responses? Brown bear responses after repeated
535 approaches by humans on foot. *Biol Conserv*, 232, 228–237.
- 536 Ordiz, A., Støen, O.-G., Sæbø, S., Sahlén, V., Pedersen, B.E., Kindberg, J., *et al.* (2013b).
537 Lasting behavioural responses of brown bears to experimental encounters with humans. *J*
538 *Appl Ecol*, 50, 306–314.
- 539 Oriol-Cotterill, A., Valeix, M., Frank, L.G., Riginos, C. & Macdonald, D.W. (2015). Landscapes
540 of Coexistence for terrestrial carnivores: the ecological consequences of being
541 downgraded from ultimate to penultimate predator by humans. *Oikos*, 124, 1263–1273.
- 542 Palmer, M.S., Fieberg, J., Swanson, A., Kosmala, M. & Packer, C. (2017). A ‘dynamic’
543 landscape of fear: prey responses to spatiotemporal variations in predation risk across the
544 lunar cycle. *Ecol Lett*, 20, 1364–1373.
- 545 Plummer, M. (2003). JAGS: A program for analysis of Bayesian graphical models using Gibbs
546 sampling. In: *Proceedings of the 3rd international workshop on distributed statistical*
547 *computing*. Vienna, Austria.
- 548 Ridout, M.S. & Linkie, M. (2009). Estimating overlap of daily activity patterns from camera trap
549 data. *JABES*, 14, 322–337.
- 550 Royle, J.A., Chandler, R.B., Sollmann, R. & Gardner, B. (2013). *Spatial Capture-Recapture*.
551 Academic Press, Waltham, USA.

- 552 Royle, J.A. & Dorazio, R.M. (2008). *Hierarchical Modeling and Inference in Ecology: The*
553 *Analysis of Data from Populations, Metapopulations and Communities*. Academic Press,
554 London, UK.
- 555 Salo, P., Banks, P.B., Dickman, C.R. & Korpimäki, E. (2010). Predator manipulation
556 experiments: impacts on populations of terrestrial vertebrate prey. *Ecol Monogr*, 80, 531–
557 546.
- 558 Schmitz, O.J., Beckerman, A.P. & O'Brien, K.M. (1997). Behaviorally mediated trophic
559 cascades: effects of predation risk on food web interactions. *Ecology*, 78, 1388–1399.
- 560 Schuette, P., Creel, S. & Christianson, D. (2013). Coexistence of African lions, livestock, and
561 people in a landscape with variable human land use and seasonal movements. *Biol*
562 *Conserv*, 157, 148–154.
- 563 Smith, J.A., Suraci, J.P., Clinchy, M., Crawford, A., Roberts, D., Zanette, L.Y., *et al.* (2017).
564 Fear of the human 'super predator' reduces feeding time in large carnivores. *Proc R Soc*
565 *B*, 284, 20170433.
- 566 Smith, J.A., Thomas, A.C., Levi, T., Wang, Y. & Wilmers, C.C. (2018). Human activity reduces
567 niche partitioning among three widespread mesocarnivores. *Oikos*, 127, 890–901.
- 568 Smith, J.A., Wang, Y. & Wilmers, C.C. (2015). Top carnivores increase their kill rates on prey
569 as a response to human-induced fear. *Proc R Soc B*, 282, 20142711.
- 570 Stankowich, T. (2008). Ungulate flight responses to human disturbance: A review and meta-
571 analysis. *Biol Conserv*, 141, 2159–2173.
- 572 Stankowich, T. & Blumstein, D.T. (2005). Fear in animals: a meta-analysis and review of risk
573 assessment. *Proc R Soc B*, 272, 2627–2634.
- 574 Su, Y.-S. & Yajima, M. (2015). R2jags: A Package for Running jags from R. *R package version*
575 *0.5-7*.
- 576 Suraci, J.P., Clinchy, M., Dill, L.M., Roberts, D. & Zanette, L.Y. (2016). Fear of large carnivores
577 causes a trophic cascade. *Nat Commun*, 7, 10698.
- 578 Suraci, J.P., Clinchy, M. & Zanette, L.Y. (2017). Do large carnivores and mesocarnivores have
579 redundant impacts on intertidal prey? *PLOS ONE*, 12, e0170255.
- 580 Suraci, J.P., Frank, L.G., Oriol-Cotterill, A., Ekwanga, S., Williams, T.M. & Wilmers, C.C.
581 (2019). Behavior-specific habitat selection by African lions may promote their
582 persistence in a human-dominated landscape. *Ecology*, e02644.

583 Tucker, M.A., Böhning-Gaese, K., Fagan, W.F., Fryxell, J.M., Moorter, B.V., Alberts, S.C., *et*
584 *al.* (2018). Moving in the Anthropocene: Global reductions in terrestrial mammalian
585 movements. *Science*, 359, 466–469.

586 Valeix, M., Hemson, G., Loveridge, A.J., Mills, G. & Macdonald, D.W. (2012). Behavioural
587 adjustments of a large carnivore to access secondary prey in a human-dominated
588 landscape. *J Appl Ecol*, 49, 73–81.

589 Venter, O., Sanderson, E.W., Magrath, A., Allan, J.R., Beher, J., Jones, K.R., *et al.* (2016).
590 Sixteen years of change in the global terrestrial human footprint and implications for
591 biodiversity conservation. *Nat Commun*, 7, 12558.

592 Wang, Y., Allen, M.L. & Wilmers, C.C. (2015). Mesopredator spatial and temporal responses to
593 large predators and human development in the Santa Cruz Mountains of California. *Biol*
594 *Conserv*, 190, 23–33.

595 Wang, Y., Smith, J.A. & Wilmers, C.C. (2017). Residential development alters behavior,
596 movement, and energetics in an apex predator, the puma. *PLOS ONE*, 12, e0184687.

597 Wilmers, C.C., Wang, Y., Nickel, B., Houghtaling, P., Shakeri, Y., Allen, M.L., *et al.* (2013).
598 Scale dependent behavioral responses to human development by a large predator, the
599 puma. *PLoS ONE*, 8, e60590.

600 Zanette, L.Y., Clinchy, M. & Suraci, J.P. (2014). Diagnosing predation risk effects on
601 demography: can measuring physiology provide the means? *Oecologia*, 176, 637–651.

602 Zanette, L.Y., White, A.F., Allen, M.C. & Clinchy, M. (2011). Perceived predation risk reduces
603 the number of offspring songbirds produce per year. *Science*, 334, 1398–1401.

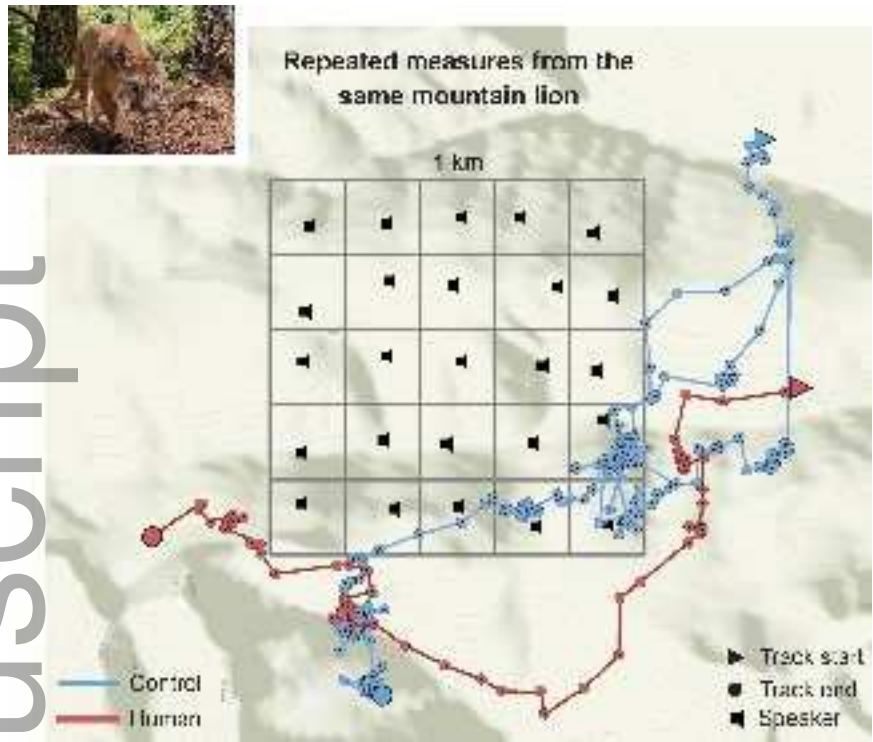
604
605

606 **Figure Legends**

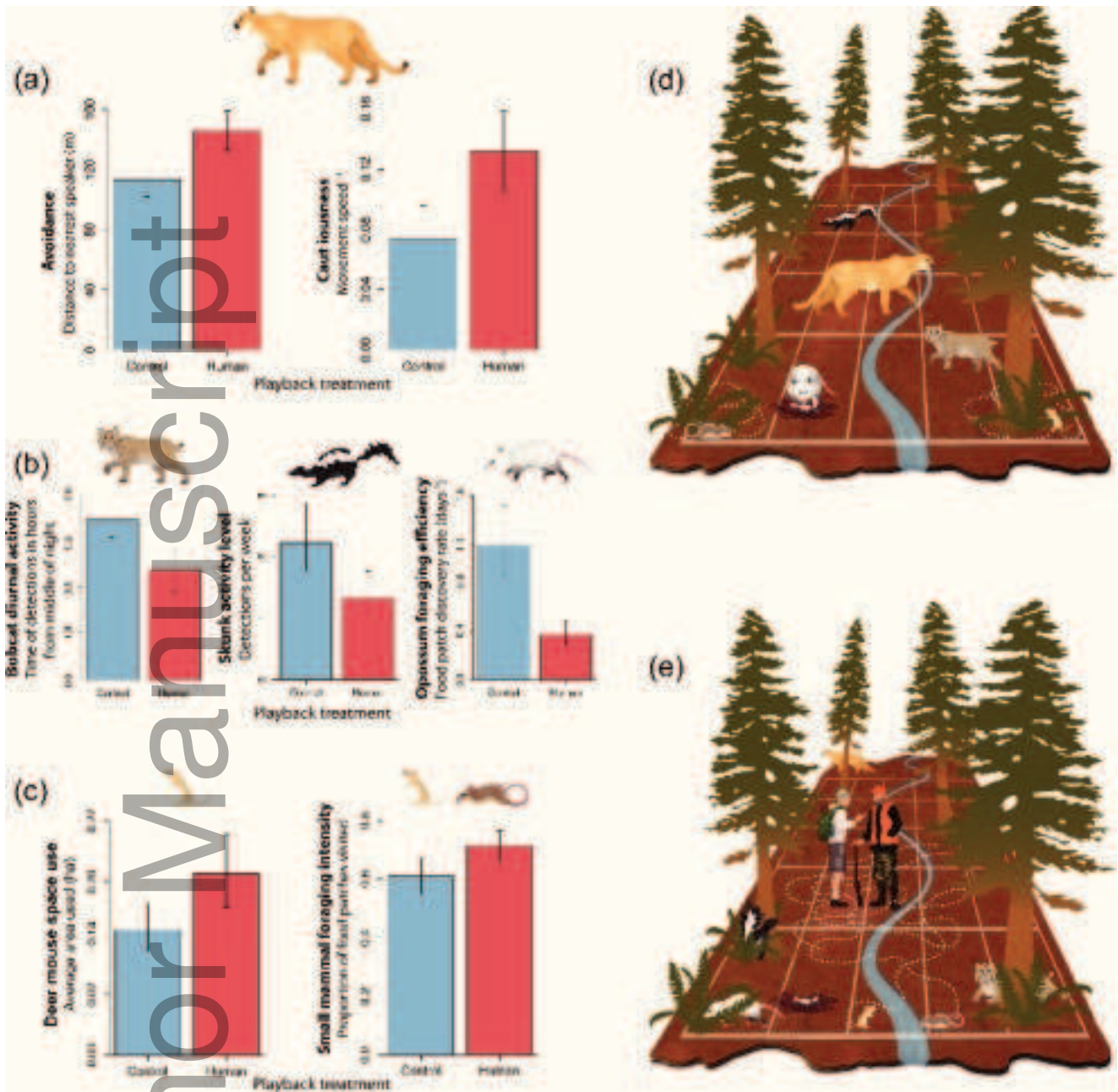
607 **Fig. 1.** Example of the landscape-scale impacts of fear of humans on mountain lion behavior,
608 illustrated by repeated-measures movement tracks from a single mountain lion during the control
609 (blue) and human (red) treatments. Points are 5-min GPS fixes, and connecting lines illustrate
610 the approximate movement path. Black speaker icons denote playback speaker locations and the
611 grey grid illustrates the 1-km² experimental site. Photo © Sebastian Kennerknecht.

612

613 **Fig. 2.** Fear of humans has landscape-scale impacts on wildlife across multiple trophic levels. **(a)**
614 Fear of humans affects mountain movement behavior. Mountain lion avoidance behavior (left
615 panel) is shown as average distance (m) to the nearest playback speaker and cautiousness (right
616 panel) is shown as the inverse of average movement speed (mins/m). Bar plots illustrate means \pm
617 SEM. N = 10 control and 7 human. **(b)** Fear of humans suppresses medium-sized carnivore
618 behavior. Bobcat diurnal activity from camera trap detections (left panel; means \pm SEM; n = 26
619 control and 18 human) is shown as time (h) from the middle of the night. Skunk overall activity
620 level (middle panel) is shown as posterior mean and 95% credible intervals for number of
621 detections per week on camera traps. Opossum foraging efficiency (right panel; means \pm SEM; n
622 = 10 control and 10 human) is shown as rate of discovery (days^{-1}) of provisioned food patches.
623 **(c)** Suppression of larger mammals induced by fear of humans benefits small mammals. Deer
624 mouse space use (left panel) is shown as posterior mean and 95% credible intervals of average
625 area (ha) used. Small mammal (deer mouse and woodrat) foraging intensity (right panel; mean \pm
626 SEM; n = 64 control and 73 human) is shown as proportion of provisioned food patches visited
627 on a given night. All bar plots illustrate behaviors during control (blue) and human (red)
628 playback treatments. **(d)** and **(e)** conceptual illustrations of the landscape-scale effects of fear of
629 humans on wildlife communities. Where the human apex predator is absent or rare **(d)**, large and
630 medium-sized carnivores exhibit greater movement (mountain lion on grid), activity (bobcats
631 and skunks active), and foraging (opossum eating a bird nest), while small mammals exhibit
632 reduced space use (constricted movement paths, shown as dashed lines). Where humans are
633 present **(e)**, fear of humans suppresses the activity, foraging, and/or habitat use of large and
634 medium-sized carnivores, while small mammals increase their total space use and foraging
635 intensity. Original artwork by Corlis Schneider.



ele_13344_f1.tif



ele_13344_f2.tif