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Original Article

Fearlessness towards extirpated large carnivores may exacerbate the impacts of naïve mesocarnivores

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By suppressing mesocarnivore foraging, the fear large carnivores inspire can be critical to mitigating mesocarnivore impacts. Where large carnivores have declined, mesocarnivores may quantitatively increase foraging, commensurate with reductions in fear. The extirpation of large carnivores may further exacerbate mesocarnivore impacts by causing qualitative changes in mesocarnivore behavior. Error management theory suggests that, where predators are present, prey should be biased towards over-responsiveness to predator cues, abandoning foraging in response to both predator cues and benign stimuli mistaken for predator cues (false-positives). Where predators are absent, prey may avoid these foraging costs by becoming unresponsive (naïve) to both predator cues and false-positives. If naïveté occurs in mesocarnivores where large carnivores have been extirpated, it could substantively exacerbate their impacts, as “fearless” mesocarnivores may engage in virtually unrestricted foraging. We tested the naïveté of raccoons (*Procyon lotor*) to extirpated large carnivores in the context of a larger experiment demonstrating that fear of large carnivores can mediate mesocarnivore impacts. Raccoon responsiveness to playbacks of their extirpated large carnivore predators (cougars, *Puma concolor*, bears, *Ursus americanus*) was significantly less than to the only extant large carnivore predator (dogs), and was no greater than to non-predators (“seals”; *Phoca vitulina*, *Eumetopias jubatus*). Raccoons failed to recognize their now extirpated predators as threatening, spending as much time foraging as when hearing non-predators, which we estimate has substantive impacts, based on results from the larger experiment. We discuss the potentially powerful role of “fearlessness” in exacerbating mesocarnivore impacts in systems where large carnivores have been lost.

Key words: antipredator behavior, ecology of fear, mesopredator release, playback experiment, predation risk, predator naïveté.

INTRODUCTION

The fear (perceived predation risk) that large carnivores inspire in mesocarnivores may itself be powerful enough to initiate cascading effects across food webs, impacting the abundance of species at multiple lower trophic levels (Prugh et al. 2009; Ritchie and Johnson 2009; Ripple et al. 2014). This was recently experimentally demonstrated by Suraci et al. (2016a), who reported that manipulating fear itself using month-long playbacks of large carnivore (dog, *Canis lupus familiaris*) vocalizations dramatically suppressed mesocarnivore (raccoon; *Procyon lotor*) foraging to the benefit of the mesocarnivore’s prey, which in turn affected additional trophic levels. These results

corroborate that the fear large carnivores inspire is an important component of their role in regulating biodiversity by mitigating mesocarnivore impacts (Letnic et al. 2009, 2012; Ripple et al. 2014), and indicate that these impacts may thus be exacerbated when mesocarnivores are partially “released” from fear following reductions in large carnivore numbers (Prugh et al. 2009; Ritchie and Johnson 2009; Ripple et al. 2014). Where a species of large carnivore has been entirely extirpated, there may be an additional reduction in antipredator behavior if the mesocarnivore ceases to respond in any way to cues similar to those of its now extirpated predator, thereby becoming “fearless” (Berger et al. 2001; Blumstein 2002; Blumstein and Daniel 2005). The accompanying increase in time spent foraging could potentially lead to even greater impacts on lower trophic levels, though this has yet to be explored as a further adverse consequence of the ongoing extirpations of large carnivores occurring worldwide (Estes et al. 2011; Ripple et al. 2014).

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Being fearful of large carnivores may impose substantial costs on mesocarnivores by limiting the time available for foraging (Lima and Dill 1990; Brown and Kotler 2004), and these costs should be minimized when the actual risk posed by large carnivores has been removed. Suraci et al. (2016a) reported that responding to large carnivore playbacks led to a 66% reduction in mesocarnivore foraging, and earlier playback experiments have demonstrated that the suppression of foraging caused by the fear of predators can lead to a substantial (at least 40%) reduction in annual reproduction in wildlife (Zanette et al. 2011, 2013). Animals in these playback experiments were responding to the cues of non-existent predators, illustrating the potentially significant costs of responding to “false positives” (Type II error *sensu* Blumstein 2006; Johnson et al. 2013), that is, mistakenly responding to a cue as being from a predator when it is not. In these experiments the researchers intentionally tricked the subjects, but animals are often “tricked” by false-positives in nature. Indeed responding to innocuous environmental stimuli mistakenly perceived as predator cues appears common among wildlife, with studies reporting substantial (up to a 75%) false positive response rates in some wildlife populations (Cresswell et al. 2000; Hare and Atkins 2001; Beauchamp and Ruxton 2007), and may result from the frequent overlap in vocalizations, odor, and movement between predator and non-predator species.

Error management theory, which seeks adaptive explanations for biases in decision making (Johnson et al. 2013; Orrock et al. 2015), suggests that interrupting foraging to mistakenly respond to a benign cue may be adaptive where predators are present and the resulting cost of missing a meal must therefore be traded off against actually being killed, should the cue prove true (i.e., where the cost of a “false negative” greatly outweighs that of a false positive). This asymmetry in outcomes explains why animals commonly show a behavioral bias toward overestimating predation risk (Bouskila and Blumstein 1992; Foster and Kokko 2009; Johnson et al. 2013). Where predator numbers have been reduced (e.g., following large carnivore declines), prey may be expected to respond to relaxed predation risk by increasing their foraging behavior, but remain fully responsive to cues associated with the still present predators, and therefore continue to respond to false positives. However, where a predator has been lost completely, but potential sources of false positives (e.g., non-predator species with vocalizations similar to those of the now absent predator) remain, the substantial costs of responding to false positives may lead to a qualitative shift in prey behavior, causing them to effectively “turn off” their responsiveness to cues that could be mistaken for those of their now absent predator. Doing so would reduce false positives to near zero, and thus minimize the likelihood of expressing inappropriate and costly antipredator behaviors (Blumstein 2002; Blumstein and Daniel 2005; Blumstein 2006). The corollary of eliminating time spent responding to false positives is that there is that much more time available for foraging (Lima and Dill 1990; Brown and Kotler 2004).

A lack of responsiveness to predator cues, known as predator naiveté, has repeatedly been reported among prey populations that have been isolated from predators for thousands of years (Blumstein et al. 2000; Blumstein and Daniel 2005; Orrock 2010) and was referred to by Darwin (1839) when describing the “tame-ness” of species on the Galápagos Islands. Yet the loss of predator fear may occur much more quickly, for instance following contemporary introductions of prey species to predator-free habitat (e.g., Blumstein 2002) or human-caused predator extirpation (e.g., Berger 2007). The rapid loss of fear in wildlife following the extirpation

of large carnivores has been experimentally demonstrated in several ungulate species (bison *Bison bison*, caribou *Rangifer tarandus*, elk *Cervus elaphus*, and moose *Alces alces*), shown to be naïve to cues associated with wolves (*Canis lupus*) and grizzly bears (*Ursus arctos*) after as little as 50 years of separation (Berger 1999, 2007; Berger et al. 2001; Sand et al. 2006).

The ongoing decline of large carnivores in many parts of the world has raised major conservation concerns, in part due to the resultant weakening in top-down control of mesocarnivores (Estes et al. 2011; Ripple et al. 2014), which has led to reductions in abundance and diversity at lower trophic levels, a phenomenon known as mesopredator release (Crooks and Soulé 1999; Johnson et al. 2007; Prugh et al. 2009; Ripple et al. 2013; Suraci et al. 2014). Reduced fear in mesocarnivores following large carnivore declines has been implicated in mesopredator release, as the relaxation of predation risk may allow mesocarnivores to increase the temporal and spatial extent of foraging, thus increasing impacts on their prey (Prugh et al. 2009; Ritchie and Johnson 2009; Brook et al. 2012; Letnic et al. 2012). What has not been considered are the effects that the complete extirpation of species of large carnivores may have on mesocarnivore behavior. If mesocarnivores fail to recognize and respond to cues of extirpated large carnivores (i.e., are predator naïve, as has been shown in large herbivores; Berger 1999, 2007; Berger et al. 2001; Sand et al. 2006), additional impacts may result from mesocarnivores becoming “fearless” and ceasing to exhibit antipredator behavior in response to false positives (e.g., non-predator cues similar to those of the extirpated large carnivores).

The necessary first step in establishing whether mesocarnivore fearlessness exacerbates the impacts of mesopredator release is to determine how the extirpation of species of large carnivores affects the responsiveness of mesocarnivores to predator cues. To accomplish this first step, we experimentally tested whether raccoons, a model mesocarnivore, are naïve to the cues of their now extirpated large carnivore predators in the Gulf Islands of British Columbia, Canada. This work was conducted in the context of the larger experiment reported in Suraci et al. (2016a), noted above, which quantified the extent to which the fear of large carnivores mediates mesocarnivore impacts in this system. Suraci et al. (2016a) showed that experimentally restoring the fear of large carnivores largely reversed raccoon impacts on intertidal fish and invertebrates by suppressing raccoon foraging, allowing populations of these prey species to increase in abundance. With the exception of dogs (which have always been kept by the aboriginal peoples here; Hanson 1995), all native large carnivores that were formerly present throughout the Gulf Islands (cougars *Puma concolor*, black bears *Ursus americanus* [hereafter “bears”], and wolves) were extirpated by humans last century (Golumbia 2006; Martin et al. 2011; Suraci et al. 2014). Cougars and bears are known to harass and kill raccoons where these large carnivores persist, including on nearby Vancouver Island, where raccoons are heavily preyed-upon by cougars, occurring in more than a third of sampled cougar scats (Hansen et al. 2010). Here we report the relative fearfulness that Gulf Islands raccoons demonstrated in reaction to playbacks of both extirpated (cougar and bear) and extant (dog) large carnivore predators, and non-predator controls (“seals”; harbor seals, *Phoca vitulina*; Steller sea lions, *Eumetopias jubatus*). We discuss the implications of our results regarding the impacts mesocarnivore fearlessness may have in this system, and the growing number of other systems worldwide where large carnivores have recently been lost or face imminent extirpation.

MATERIALS AND METHODS

Overview of experimental design and study area

To determine whether raccoons on the Gulf Islands are naïve to their extirpated large carnivore predators, we experimentally tested the antipredator responses of diurnally active, intertidal-foraging raccoons to playbacks of the vocalizations of 2 extirpated large carnivore predators (cougar, bear), comparing these with their reactions to an extant large carnivore predator (dog) and extant non-predators (seals). We previously reported that this population of raccoons responds fearfully to dogs, either leaving the intertidal or significantly reducing foraging in favor of vigilance, which we determined by comparing raccoon responses to dog and seal playbacks in the larger experiment described above (Suraci et al. 2016a). Consequently, we were able to confidently classify raccoons as naïve to their extirpated large carnivore predators (i.e., perceiving cougars and bears as non-threatening), if their antipredator responses were significantly less than to their extant predator (dog) and not significantly different from their responses to non-predators (seals; Blumstein et al. 2008; Hettena et al. 2014). We have also found that the cougar and bear playbacks used here elicited significant behavioral responses in experiments on other mammalian carnivores—the cougar playbacks having elicited investigative behaviors and aggression in black bears (Suraci et al. *in prep*), and the bear playbacks having inspired fear in badgers (*Meles meles*; Clinchy et al. 2016). Thus we could also be confident that mammalian carnivores perceive these playbacks as simulating the presence of the large carnivores in question (cougars and bears), and if raccoons responded no more strongly to these same cougar and bear playbacks than to non-predator playbacks, it is because the raccoons failed to recognize cues from cougars and bears as threatening, and are thus naïve with respect to these extirpated large carnivore predators.

Where raccoons co-occur with cougars and bears, there is ample reason to expect them to be exposed to these predators' vocalizations, as both large carnivore species vocalize regularly. Cougar kittens stay with their mothers for up to 2 years and mothers and kittens call to one another regularly to maintain contact while patrolling the family's home range (Logan and Sweanor 2010). Adult cougars of both sexes are also known to vocalize frequently when engaged in reproductive behaviors; individuals (particularly females) will caterwaul (a loud, often high-pitched call) to advertise their reproductive status (Allen et al. 2014), and breeding pairs vocalize repeatedly during multiday mating associations (Beier et al. 1995). Black bears are known to be highly vocal when foraging in proximity to conspecifics (Herrero 1983), and multiple bears commonly congregate in intertidal habitats at low tide in areas where this species persists and coexists with raccoons (e.g., on nearby Vancouver Island; JPS, pers. obs.). As with cougars, bear cubs stay with their mothers for more than a year and mothers and cubs vocalize to one another regularly (Jonkel and McTaggart-Cowan 1971).

This work was conducted between 25 May 2013 and 16 September 2013 in the Gulf Islands of British Columbia, Canada. We conducted a total of 123 trials on 3 small Gulf Islands (Portland, 220 ha, 48°43'35"N, 123°22'22"W; Wallace, 115 ha; 48°56'36"N, 123°33'13"W; Coal, 141 ha, 48°41'5"N, 123°22'35"W). Portland and Wallace Islands consist primarily of National and Provincial parkland (respectively) and Coal is a private island with a single residence (Suraci et al. 2016a). Consistent with there being differences between islands in the type and level of human disturbance, there were differences between islands in raccoon responsiveness to

playbacks, as we report, making it necessary to consider these differences in analysing the data. However, this in no way confounded the results, as these island-level differences in responsiveness were consistent across playback treatments (see below). Trials of all 4 playback treatments (cougar, bear, dog, and seal) were conducted on 2 islands (Portland and Wallace) whereas, because our access to the third island (Coal) was restricted, we conducted trials of only 3 treatments (cougar, dog, and seal) on Coal Island. Consequently, we report the results of separate analyses comparing: 1) cougar, dog, and seal trials conducted on all 3 islands; and 2) bear, dog, and seal trials conducted on Portland and Wallace Islands.

Implementing the playbacks

We prepared 10-s playbacks of large carnivore predator and non-predator vocalizations from recordings obtained from online audio and video databases and library archives. We used multiple exemplars of each playback type (3 cougars, 3 bears, 10 dogs, and 5 seals) and ensured that there were no frequency differences between playback types, using Anova to compare each of 4 frequency characteristics (average, maximum, minimum, and peak frequency; all $P \geq 0.12$). Playbacks were broadcast at a mean (\pm SD) volume of 78.1 (\pm 3.3) dB at 1 m, with no differences in volume between playback types (1-way Anova, $P = 0.39$). All playbacks were broadcast using identical speakers (Nexxtech Mini Cube 2.0, The Source, Barrie, ON, Canada) and mp3 players (Model MP301, Coby Electronics Corp., Lake Success, NY).

Field procedures

All trials were conducted between 1 h after sunrise and 1 h before sunset. We located diurnally active raccoons foraging in the intertidal during transects of the circumference of an island, and broadcast a randomly selected playback from a concealed location. We recorded the focal raccoon's behavior for 3 min prior to and up to 3 min after the playback using a digital video camera (Model DCR-SX45 Handycam, Sony Canada Ltd., Toronto, ON, Canada). For each trial, the observer (D.J.R. or J.P.S.), time of day, tide height, and habitat variables that could potentially affect the raccoon's ability to hear the playback—rainfall (on a qualitative 4-point scale), wind speed (Beaufort scale), and shoreline wave action (on a qualitative 4-point scale)—were recorded. None of these variables differed between playback types (Kruskal-Wallis tests: all $P \geq 0.27$). As the presence of conspecifics could potentially affect the focal raccoon's behavior, we also recorded the number of conspecifics within 25 m and 50 m of the focal animal and found no difference between playback types (Kruskal-Wallis tests: all $P > 0.22$). Finally, we used a rangefinder (Sport 450, Bushnell Outdoor Products, Overland Park, KS) to measure the distance between the speaker and the focal raccoon at the time of the playback. We found that raccoons were on average closer to the speaker when bear playbacks were broadcast (mean \pm SD = 26.4 \pm 13.9 m), compared to dog (32.0 \pm 15.0 m) or seal playbacks (30.5 \pm 23.1 m; Anova, $P = 0.032$), but this actually reinforces rather than confounds our findings with respect to the relative strength of raccoon responses to each of the treatments, as reported below.

We conducted playback trials at multiple sites on each island, with sites separated by a median linear distance of 266 m, comparable to the spacing of sampling points (273 m) commonly utilized in live-trapping raccoons (e.g., Gehrt and Prange 2007). We conducted (at most) one trial per day at a given site, and across the entire study period, each playback treatment was presented

only once at a site. The minimum distance between trials of the same treatment did not differ between playback treatments (Anova, $P = 0.17$). All fieldwork was approved by the Animal Care Committee of the University of Western Ontario (permit number 2010–024 to L.Y.Z.) and conforms to the legal requirements of Canada.

Scoring behavior

A single researcher (D.J.R.), blind to the playback treatment, reviewed the videos of all trials, scoring the focal raccoon's behavior during 1 min immediately prior to and 1 min immediately following the start of the playback (Blumstein et al. 2008). We also noted whether or not the raccoon abandoned foraging and left the intertidal within the 3 min immediately following the playback. We focused on 3 measures of the raccoon's behavioral response. We first categorized 1) whether or not the raccoon left the intertidal following the playback. For those individuals that remained in the intertidal for at least 1 min following the playback, we quantified the time spent vigilant or foraging before and after the playback (see Suraci et al. 2016a for details on scoring vigilance and foraging from videos), and then calculated 2) the change in vigilance and 3) the change in foraging, in the 1-min immediately following the playback relative to the 1 min immediately prior to the playback; thus providing a repeated-measures value reflecting the degree to which each individual increased or decreased vigilance/foraging in response to the playback (following Blumstein et al. 2008). Prior to playbacks being broadcast, raccoons spent most (72%) of their time foraging, with other behaviors each occupying 6% or less of their time. Following the playbacks, among those raccoons that did not leave the intertidal, there was a substantial increase in the proportion of time spent vigilant (31%) and a corresponding decrease in time spent foraging (36%), with other activities again each occupying 6% or less of their time. Because behaviors other than vigilance or foraging each occupied very little of each raccoon's time and are less obviously indicative of the level of threat perceived, we restricted our analyses to just these 2 measures of the change in raccoon time allocation in response to the playbacks.

Statistical analyses

We tested for treatment effects on the likelihood of a raccoon leaving the intertidal following the playback by conducting Treatment \times Island log-linear analyses, first testing among all 3 treatments (locally extinct large carnivore of interest [cougar or bear] compared to both dog and seal), and then conducting 2 subsequent tests, comparing the extinct large carnivore of interest (cougar or bear) versus the dog and seal playbacks separately, using Bonferroni's correction to judge the significance of these 2 subsequent tests ($P_{\text{crit}} = 0.025$). These analyses revealed almost significant differences between islands in the likelihood of leaving the intertidal ($0.10 > P > 0.05$) but no significant Treatment by Island interactions (all $P > 0.40$), the pattern of response to the treatments thus being consistent across islands.

We tested for treatment effects on the change in vigilance and the change in foraging using 2-way Anovas (Treatment \times Island) to compare all 3 treatments, followed by Dunnett's tests (Dunnett 1964) comparing the extinct large carnivore of interest (cougar or bear) versus the dog and seal playbacks separately. There was a significant difference among islands in the change in vigilance in both the cougar, dog, and seal ($P = 0.030$) and the bear, dog, and seal ($P = 0.014$) analyses, but no treatment by island interactions (all $P > 0.10$), and there were no significant island differences in the

change in foraging (all $P > 0.48$); the pattern of change in vigilance and foraging in response to the treatments being consistent across islands. Prior to analysis, these data were Box–Cox transformed (Krebs 1998) and tested for normality and homogeneity of variances. Results reported below and in the figures were back-transformed to the original units to aid meaningful interpretation.

RESULTS

Comparing cougar, dog, and seal playbacks, there was a significant overall treatment effect on the likelihood of leaving the intertidal (Figure 1a; $\chi^2_2 = 13.49$, $P = 0.001$), with raccoons being significantly less likely to leave the intertidal following a cougar playback than a dog playback ($\chi^2_1 = 6.01$, $P = 0.014$), while not being significantly more likely to do so following a cougar playback than a seal playback ($\chi^2_1 = 1.16$, $P = 0.281$). Comparing the response to cougar, dog, and seal playbacks among those individuals that did not leave the intertidal, there were significant overall treatment effects on both the change in vigilance ($F_{2,50} = 8.52$, $P < 0.001$) and the change in foraging ($F_{2,50} = 7.44$, $P = 0.001$). The increase in vigilance (Figure 1b) in response to cougars was significantly less than to dogs (Dunnett's test, $P = 0.004$) and no different than to seals (Dunnett's test, $P = 0.999$). The decrease in foraging (Figure 1c) following cougar playbacks was intermediate compared to the other 2 treatments, being less than that following dogs but not significantly so (Dunnett's test, $P = 0.147$), and tending to be greater than that following seals (Dunnett's test, $P = 0.062$). The lack of difference in response to cougars and seals was not because the raccoons did not hear the playbacks; the increase in vigilance and decrease in foraging being significantly different from zero in each treatment (increase in vigilance, 95% confidence interval lower bound: dog = 20.8 s, cougar = 3.5, seal = 4.5; decrease in foraging, 95% CI upper bound: dog = -30.3, cougar = -14.5, seal = -0.6).

Comparing bears, dogs, and seals, there was a significant overall treatment effect on the likelihood of leaving the intertidal (Figure 2a; $\chi^2_2 = 9.77$, $P = 0.008$), with raccoons being significantly less likely to leave following a bear playback than a dog playback ($\chi^2_1 = 6.49$, $P = 0.011$), while being no more likely to do so following a bear than a seal playback ($\chi^2_1 = 0.02$, $P = 0.896$). Comparing the response to bear, dog, and seal playbacks among those individuals that did not leave the intertidal, there was a significant overall treatment effect on both the change in vigilance ($F_{2,45} = 3.36$, $P = 0.044$) and the change in foraging ($F_{2,45} = 4.12$, $P = 0.023$). Whereas the increase in vigilance (Figure 2b) in response to bear playbacks was somewhat but not significantly less than that to dogs (Dunnett's test, $P = 0.208$) and not significantly different than that to seals (Dunnett's test, $P = 0.723$), the decrease in foraging (Figure 2c) following bear playbacks was significantly less than that following dogs (Dunnett's test, $P = 0.018$) and no different than that following seals (Dunnett's test, $P = 0.996$). As with cougars and seals, the lack of difference in response to bears and seals was not because the raccoons did not hear the playbacks; the increase in vigilance and decrease in foraging being significantly different from zero in each treatment (increase in vigilance, 95% CI lower bound: dog = 18.2 s, bear = 9.7, seal = 5.4; decrease in head down foraging, 95% CI upper bound: dog = -25.1, bear = -4.5, seal = -2.3).

DISCUSSION

Our results demonstrate that raccoons in the Gulf Islands are naïve to cues of their now extirpated large carnivore predators, being

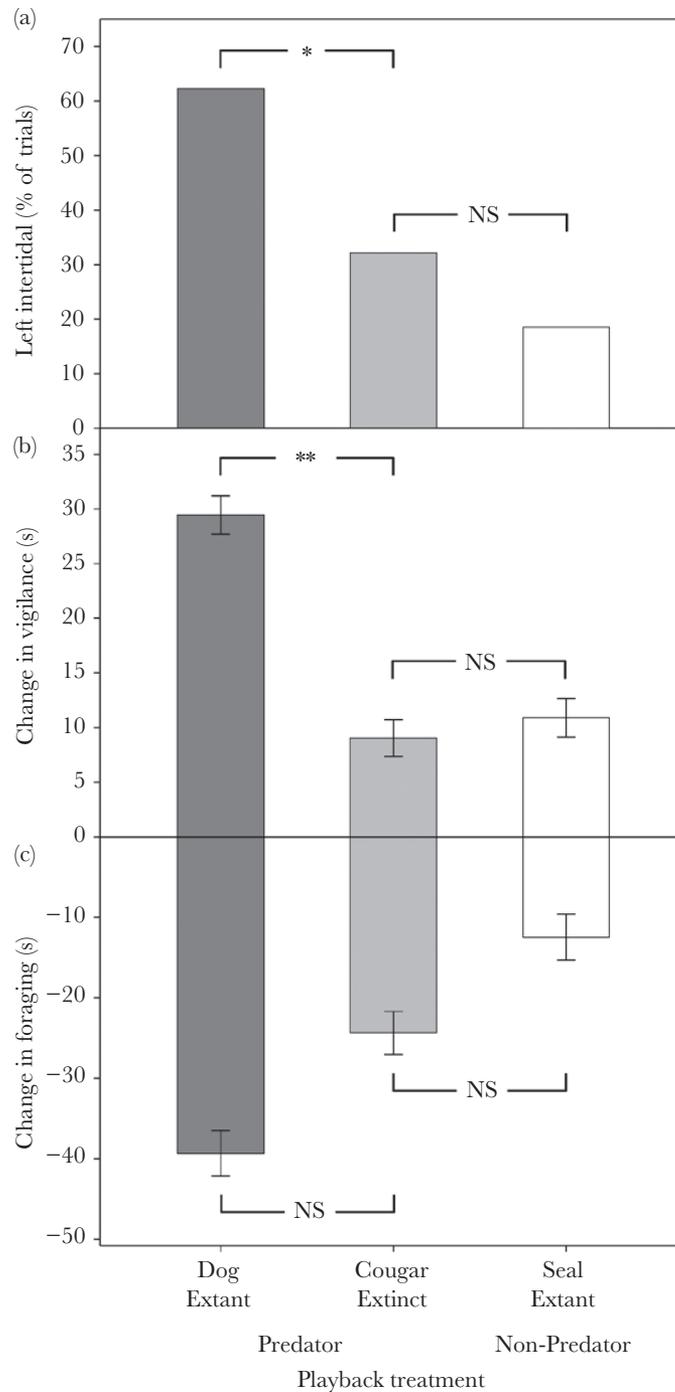


Figure 1

Responsiveness of raccoons to cougars, a now extinct large carnivore predator, relative to dogs (extant large carnivore predator) and seals (non-predator control), as illustrated by (a) the percent of all trials in which the raccoon left the intertidal for at least 1 min following the playback, (b) the mean change in vigilance, and (c) mean change in foraging in the 1 min following the playback, relative to the 1 min immediately prior to the playback. Error bars in (b) and (c) represent ± 1 SE. Significance level of the differences in paired comparisons between treatments are shown. * $P < 0.05$, ** $P < 0.01$, NS (non-significant).

significantly less responsive to cougar and bear playbacks than to playbacks of the only extant large carnivore in the Gulf Islands (dogs), while being no more responsive to cougars and bears than to non-predator (seal) playbacks. That raccoons did not respond significantly differently to cougars or bears than they did to seals demonstrates that they did not perceive cougars and bears as any more

threatening than non-predators. At least with regards to cougars and seals, the response was nonetheless not identical (Figure 1), suggesting that the raccoons perceived some difference between these cues, whereas they evidently perceived virtually no difference between the sounds of bears and seals (Figure 2). Conversely, our results unambiguously show that raccoons did differentiate cougars

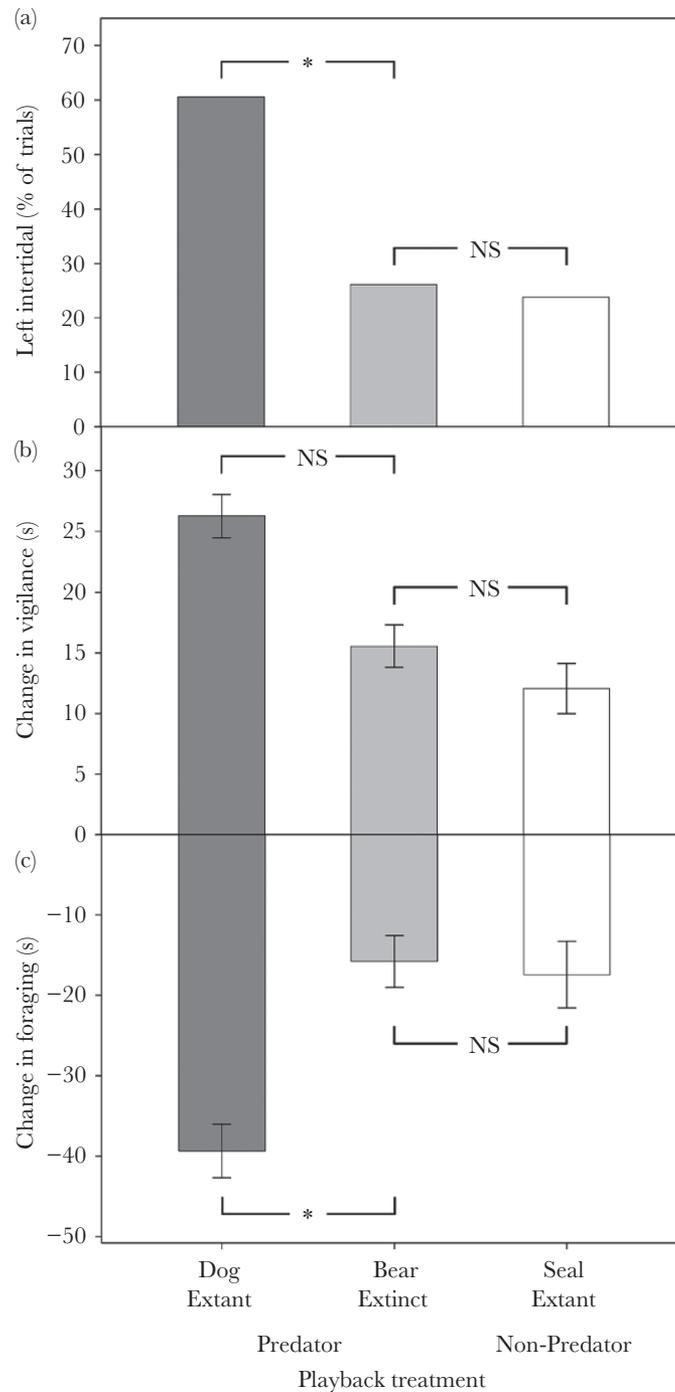


Figure 2

Responsiveness of raccoons to black bears, a now extinct large carnivore predator, relative to dogs (extant large carnivore predator) and seals (non-predator control), as illustrated by (a) the percent of all trials in which the raccoon left the intertidal, and, among those individuals that remained in the intertidal for at least 1 min following the playback, (b) the mean change in vigilance, and (c) mean change in foraging in the 1 min following the playback, relative to the 1 min immediately prior to the playback. Error bars in (b) and (c) represent ± 1 SE. Significance level of the differences in paired comparisons between treatments are shown. * $P < 0.05$, NS (non-significant).

and bears from the extant large carnivore, dogs, clearly corroborating that they failed to perceive their former large carnivore predators as threatening.

By demonstrating that raccoons are naïve to the cues of their (relatively) recently extirpated large carnivore predators, this study provides the necessary first step in exploring the role of mesocarnivore

fearlessness in contributing to the impacts associated with meso-predator release. We have previously documented that raccoons on the Gulf Islands strongly impact both terrestrial and marine communities, the abundances of nesting songbirds and intertidal and shallow subtidal crabs and fish being severely reduced where raccoons are present, relative to raccoon-absent islands (Suraci et al. 2014).

The present study suggests that raccoon fearlessness may be contributing to these impacts and, thanks to our having conducted the current experiment in conjunction with that reported in Suraci et al. (2016a), we can directly estimate the degree to which this is the case. To begin with, our results demonstrate that raccoons definitely do respond to false positives (i.e., cues mistakenly associated with predation risk; Blumstein 2006; Johnson et al. 2013), as they mistakenly fled the intertidal in response to non-predator (seal) cues 19% of the time (Figure 1a). Relative to this baseline level of responding to false positives, responding to dog-like sounds may further reduce raccoon foraging by as much as 66%, as demonstrated by their reacting to our dog playbacks (Figure 1), and Suraci et al. (2016a) reported that this reduction in foraging significantly ameliorated the impacts of raccoons on lower trophic levels. Assuming that, where raccoons are not naïve to cougars and bears, they would react as strongly to the perceived presence of these large carnivores as they did to dogs (which we suggest is reasonable given the lethality of cougars at least, as described in the Introduction), one would expect the instantaneous reductions in raccoon foraging and impacts in response to cougar and bear false positives to be of similar magnitude. Being naïve to cougars and bears, the raccoons in our study did not reduce their foraging when hearing cougar- and bear-like sounds, but instead foraged just as much as when hearing non-predator sounds. From Suraci et al. (2016a), we can estimate that this entails a 50–60% greater impact on the raccoons' prey, relative to the reduction in foraging in response to dog-like sounds. An increased impact on the raccoon's prey of up to 50–60% is thus our estimate of the added impact of fearlessness. This is an estimate of the instantaneous impact—within the 3 min following a cue. The ecological impact additionally depends upon the frequency with which raccoons hear cues that could be mistaken for those of their now absent predators (false positives), that is, how often they naturally hear cougar- and bear-like sounds.

The frequency with which Gulf Islands raccoons naturally hear cougar- and bear-like sounds could be quite high, given the evident overlap between some cougar and raccoon vocalizations, and some bear and seal vocalizations. Cougars emit a variety of vocalizations across a broad range of frequencies, including high-pitched caterwauling “screams” (Logan and Sweaner 2010; Allen et al. 2014), many of which could be mistaken for aggressive raccoon vocalizations. Bears also produce a wide range of sounds, such as “huffs” and “grunts” (Jonkel and McTaggart-Cowan 1971; Jordan 1976) that could be mistaken for the similarly wide range of sounds produced by “seals” (i.e., harbor seals and Steller sea lions; Van Parijs and Kovacs 2002; Schusterman and Van Parijs 2003). Raccoons occur at high densities on the Gulf Islands (Suraci et al. 2014) and are almost certainly very often exposed to vocalizations of aggressive conspecifics, and similarly almost certainly very often hear “seal” sounds, given the abundance of harbor seals and Steller sea lions here (Suraci et al. 2016a). Thus, where raccoons are not naïve to cougars and bears and co-exist with them in these coastal habitats, the frequency of responses to false-positives may be quite high, as has been reported in other wildlife (Cresswell et al. 2000; Hare and Atkins 2001; Beauchamp and Ruxton 2007).

Wildlife may rapidly lose their fear of predators (Blumstein 2002; Hollings et al. 2015), as has been shown for several species of ungulate in as little as 50 years after the extirpation of large carnivores (Berger 1999, 2007; Berger et al. 2001). The same may be expected to occur among mesocarnivores, which our results suggest points to the potentially widespread occurrence of mesocarnivore fearlessness, given the ongoing extirpation of large carnivores from habitats

across the globe (Ripple et al. 2014). The rapidity with which prey lose their responsiveness to predator cues may be related to both the costs of retaining non-functional antipredator behaviors (potentially high in Gulf Islands raccoons, for which the fear of large carnivores results in up to a 66% reduction in foraging; Suraci et al. 2016a) and the degree to which these behaviors are “hard-wired” (i.e., genetically determined) versus experience-dependent (Griffin et al. 2000; Blumstein 2002, 2006). Experience-dependent antipredator behaviors are substantially more labile, potentially being lost within a single generation following separation from predators (Griffin et al. 2000; Blumstein 2002, 2006), and Blumstein (2002) notes that behaviors with high opportunity costs, such as fleeing a non-existent predator, likely fall into this category. While our results do not allow us to directly test how quickly the fear of large carnivores degrades following large carnivore extirpation, they suggest that a mesocarnivore's ability to recognize the cues of a specific large carnivore species may depend, at least in part, on experience with that species.

Mesocarnivore fearlessness may provide some cause for optimism regarding the effectiveness of large carnivore reintroduction or recolonization as an ecosystem restoration tool (Ritchie et al. 2012; Suraci et al. 2016a). Naïve prey may initially experience high predation rates from recolonizing predators (Berger et al. 2001; Sand et al. 2006), suggesting that large carnivore repatriation could help to quickly mitigate mesocarnivore overabundance—a common feature of mesopredator release (Prugh et al. 2009)—if fearless mesocarnivores are easier to kill. Further, results from the ungulate studies mentioned above suggest that the rapid loss of the fear of large carnivores may imply an equally rapid reestablishment of fear following the repatriation of these top predators, as some ungulate populations have been shown to quickly regain their ability to recognize large carnivores within one generation of the large carnivore's return (Berger et al. 2001; Berger 2007; but see Sand et al. 2006). In the Gulf Islands, raccoons exhibit strong antipredator responses to the cues of domestic dogs (this study and Suraci et al. 2016a), and these behaviors may readily be generalized to native large carnivores such as cougars and bears, if these predators returned to the system (Griffin et al. 2000). Given the experimental demonstration that the fear of large carnivores can be critical to mitigating mesocarnivore impacts by suppressing foraging (Suraci et al. 2016a), the potentially rapid reestablishment of fear following large carnivore repatriation, in combination with initially high predation rates on naïve mesocarnivores, may be highly effective at stemming the severe declines in abundance and diversity that have been shown to result from mesopredator release (Johnson et al. 2007; Prugh et al. 2009; Ritchie and Johnson 2009).

The fear that large carnivores instill in their prey is a crucial component of their role in structuring communities and ecosystems (Ripple and Beschta 2004; Creel and Christianson 2008; Suraci et al. 2016a), and one which depends on the ability of prey to recognize and respond appropriately to large carnivore cues (Berger 2007; Dalerum and Belton 2015). Our data indicate that, following large carnivore extirpation, some mesocarnivore populations may not respond to these cues, becoming fearless, with potentially grave consequences for lower trophic levels. We suggest that effective conservation of terrestrial communities therefore requires maintaining or restoring appropriate antipredator behavioral responses among mesocarnivores through the protection or repatriation of their large carnivore predators (Prugh et al. 2009; Ritchie and Johnson 2009; Ritchie et al. 2012; Ripple et al. 2014).

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Suraci et al. (2016b).

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