Fear of large carnivores causes a trophic cascade

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The fear large carnivores inspire, independent of their direct killing of prey, may itself cause cascading effects down food webs potentially critical for conserving ecosystem function, particularly by affecting large herbivores and mesocarnivores. However, the evidence of this has been repeatedly challenged because it remains experimentally untested. Here we show that experimentally manipulating fear itself in free-living mesocarnivore (raccoon) populations using month-long playbacks of large carnivore vocalizations caused just such cascading effects, reducing mesocarnivore foraging to the benefit of the mesocarnivore’s prey, which in turn affected a competitor and prey of the mesocarnivore’s prey. We further report that by experimentally restoring the fear of large carnivores in our study system, where most large carnivores have been extirpated, we succeeded in reversing this mesocarnivore’s impacts. We suggest that our results reinforce the need to conserve large carnivores given the significant “ecosystem service” the fear of them provides.
large carnivores are fearsome predators that pose real and perceived threats to human life and livelihoods, which is why humans have attempted, and largely succeeded, at extirpating them everywhere. The loss of large carnivores is now being recognized as possibly humankind’s most pervasive influence on nature, in part because the fear (perceived predation risk) they inspire in other animals may constitute a significant “ecosystem service” critical to conserving biodiversity and ecosystem function. Being at the top of the food chain, large carnivores can play a dual role in structuring ecosystems by affecting both large herbivores and mesocarnivores, causing both “tri-trophic cascades” (large carnivore–herbivore–plant) and “mesopredator cascades” (large carnivore–mesopredator–mesopredator’s prey), affecting diverse species at multiple lower trophic levels. By both killing and frightening their prey, large carnivores could have a dual impact on these dual cascades, for the straightforward reason that frightened prey (in this case large herbivores and mesocarnivores) eat less. The mere presence of large carnivores may therefore give rise to a “landscape of fear,” buffering lower trophic levels from overconsumption by large herbivores and mesocarnivores. Failing to consider fear risks substantially understimating the role large carnivores play, since fear may be as or more important than direct killing in causing trophic cascades, according to current theory and experiments primarily on captive invertebrates. Given the potential for human–carnivore conflict, there have been justifiable calls for direct experimental evidence that the fear large carnivores inspire can provide a significant “ecosystem service.” The absence of such direct evidence to date is due to the challenge of experimentally manipulating fear in free-living wildlife, it being only very recently experimentally demonstrated that fear itself is powerful enough to affect wildlife population dynamics.

To test whether the fear of large carnivores can itself cause cascading effects on mesocarnivore foraging and multiple lower trophic levels, we conducted a spatially and temporally replicated field experiment in which we manipulated fear using month-long playbacks of large carnivore vocalizations (Fig. 1; Supplementary Table 1). The experiment was conducted on wild, free-living raccoons (Procyon lotor) on several small coastal Gulf Islands (BC, Canada). The raccoon is a mesocarnivore subject to much research regarding “mesopredator release.” Most of the large carnivores known to hunt (wolf (Canis lupus), cougar (Puma concolor)) or harass (black bear (Ursus americanus)) raccoons were extirpated from the Gulf Islands last century, the sole remaining large carnivore being the domestic dog (Canis lupus familiaris), which harasses and kills raccoons here, and has been present for millennia, having always been kept by local aboriginal peoples. In a previous mensurative experiment comparing Gulf Islands with and without raccoons, we documented that raccoons impact multiple marine species, reducing the abundance of intertidal crabs and fish, and even subtidal red rock crabs (Cancer productus).

To experimentally test whether the fear of large carnivores could itself mediate the impacts of raccoons on marine biota, we broadcast large carnivore predator (dog) or non-predator (local pinnipeds; harbour seal (Phoca vitulina), Steller sea lion (Eumetopias jubatus)) vocalizations over two large sections of shoreline for 1 month, and then reversed the treatments for a second month, using a repeated measures design to spatially replicate our results, which we further spatially and temporally replicated by repeating the same manipulation on a different island the following year. We assayed the immediate reaction of raccoons to the large carnivore predator and non-predator vocalizations by directly observing their reactions to 10 s playbacks, and assessed their response to the month-long playbacks using multiple video surveillance and time-lapse cameras to continuously film both experimental sections of shoreline over both entire month-long playback periods.

To test the cascading effects of our experiment on lower trophic levels, we utilized the same methods (intertidal quadrats and subtidal crab trapping) used in our previous mensurative experiment to evaluate effects on raccoon prey, and we conducted fish trapping and a mark-recapture experiment additionally quantifying effects on species not directly eaten by raccoons, that are instead a competitor (staghorn sculpin (Leptocottus armatus)) and prey (periwinkle snail (Littorina scutulata)) of the prey (red rock crab) of raccoons. Staghorn sculpins are subtidal fish that, like red rock crabs, enter the intertidal at high tide to feed on small invertebrates, but unlike red rock crabs, evidently successfully escape being eaten by raccoons. Periwinkle snails are too small to be food for raccoons but are eaten by red rock crabs, which use a distinctive method of dispatching them, permitting the level of mortality to be quantified using standard mark-recapture procedures.

Here we report significant cascading effects of the fear of large carnivores across multiple trophic levels in an intertidal food web, which effectively reversed the impacts of mesocarnivore populations on marine biota by markedly suppressing mesocarnivore foraging. These results indicate that the fear large carnivores inspire in their prey can account for a major component of their role in structuring ecosystems, reinforcing the value of large carnivore conservation in ensuring the continuation of this critical ecosystem service.

**Results**

**Cascading effects of the fear of large carnivores.** Fear of large carnivores dramatically reduced mesocarnivore foraging (Fig. 2; Supplementary Tables 2 and 3). The immediate reaction of raccoons to the 10 s predator playbacks was to either abandon foraging entirely by leaving the intertidal (Fig. 2a) or reduce foraging (Fig. 2b) and increase vigilance. Critically, these same responses persisted throughout the month-long playbacks. Large
carnivore playbacks caused raccoons to spend less time in the intertidal (Fig. 2c), and less time feeding when they were present (Fig. 2d), with the cumulative consequence that they spent 66% less time foraging over the course of the month. This dramatic reduction in mesocarnivore foraging in turn dramatically benefitted the mesocarnivore’s prey (Fig. 3; Supplementary Tables 4 and 5). Following the month-long large carnivore playbacks, there were 97% more intertidal crabs (Fig. 3a), 81% more intertidal fish (Fig. 3b), 59% more polychaete worms (Fig. 3c) and 61% more subtidal red rock crabs (Fig. 3d; Supplementary Fig. 1) compared with after the non-predator playbacks. Finally, fear of large carnivores clearly had cascading effects on multiple lower trophic levels (Fig. 1), as the reduction in raccoon foraging (Fig. 2c,d) that produced the increased relative abundance of red rock crabs (Fig. 3d) was associated with a decreased abundance of the red rock crab’s competitor (staghorn sculpin; Fig. 4a) and led to lower survival of the red rock crab’s prey (periwinkle snail; Fig. 4b; Supplementary Table 6).

Discussion

Our results unambiguously experimentally demonstrate that the fear of large carnivores can itself cause a trophic cascade. Manipulating fear itself—by hanging a speaker from a tree—caused cascading effects on predation and competition at multiple trophic levels in the ocean (Fig. 1). Moreover, there were likely many more effects than we measured, potentially cascading down to the level of primary producers, since red rock crabs are themselves significant predators and periwinkle snails are significant grazers (Supplementary Discussion).

Our results additionally demonstrate that failing to consider the fear large carnivores inspire risks significantly underestimating their role, given the striking magnitude of the effects (Figs 3 and 4), and that these effects were comparable in magnitude to those documented in our previous mensurative experiment comparing islands with and without raccoons. The presence of raccoons on an island reduces the respective abundance of intertidal crabs and fish, and subtidal red rock crabs, by 90%, 94% and 38% (ref. 22), impacts all reversed by the 97%, 81% and 61% relative increase in each (Fig. 3) resulting from the reduction in raccoon foraging caused by the fear of large carnivores (Fig. 2). That the fear of large carnivores could itself be powerful enough to reverse these impacts correlates with the fact that the human extirpation of most large carnivores from the Gulf Islands means raccoons here no longer have much to fear, and act accordingly, as they forage night and day (being more normally nocturnal) far from cover (deep into the intertidal) and rarely look up from eating, spending 1 s vigilant per minute (Methods). Our experiment reversed this now unrestrained foraging by restoring the fear of large carnivores to a system from which it has largely been lost, revealing the significance of the ecosystem service the presence of the now extirpated large carnivores.

Figure 2 | Fear of large carnivores reduced mesocarnivore foraging. (a) Probability of remaining in the intertidal (% of trials; log-linear test, $\chi^2 = 11.96$, $P = 0.001$; $n = 45$ (predator) and 27 (non-predator)), and (b) time spent foraging (out of 60 s; ANOVA, $F_{1,36} = 15.85$, $P < 0.001$; $n = 22$ and 17) immediately following 10 s predator and non-predator playbacks. (c) Time spent in the intertidal (per occurrence on camera; Linear Mixed Effects Model (LMM), Likelihood Ratio (LR) $\chi^2 = 9.66$, $P = 0.002$; $n = 51$ and 43), and (d) proportion of time spent foraging (per occurrence on camera; LMM, LR $\chi^2 = 11.86$, $P = 0.001$; $n = 62$ and 52) during month-long predator and non-predator playbacks. Values are means $\pm$ s.e.m.

Figure 3 | Fear of large carnivores benefitted the mesocarnivore’s prey. Abundance of (a) intertidal crabs (Quasi-Poisson Generalized Linear Model (GLM), $F_{1,36} = 12.11$, $P = 0.001$; $n = 20$ (predator) and 20 (non-predator)), (b) intertidal fish (Poisson GLM, Likelihood Ratio $\chi^2 = 5.15$, $P = 0.023$; $n = 20$ and 20), (c) intertidal polychaete worms (Quasi-Poisson GLM, $F_{1,36} = 4.54$, $P = 0.039$; $n = 20$ and 20) and (d) subtidal red rock crabs (Poisson Generalized Linear Mixed Effects Model; Wald’s $\chi^2 = 10.83$, $P = 0.001$; $n = 20$ and 20) following month-long predator and non-predator playbacks. Values are means $\pm$ s.e.m.
 predator and non-predator playbacks. Values are means ± s.e.m.

(wolves, cougars and black bears) provided, solely through the fear they inspired.

Similar restorative effects of the fear of large carnivores have been attributed to the reestablishment of a "landscape of fear" accompanying the reintroduction or recolonization of large carnivores, and broad-scale impacts accompanying the loss of large carnivores that cannot be explained by the reduction in direct killing alone have likewise been attributed to the associated loss of the fear of large carnivores. The evidence to date that the fear of large carnivores can play a central role in structuring ecosystems comes largely from "natural experiments," and compelling alternative explanations often exist for the patterns observed. Our results in no way refute these alternatives, but our being able to cause a trophic cascade by directly manipulating fear does conclusively demonstrate such a thing is possible, and so corroborates that the fear of large carnivores can play the role attributed to it.

Experimentally manipulating the fear of large carnivores demonstrably affected mesocarnivore behaviour (Fig. 2), which in turn evidently caused a fear cascade affecting the behaviour of at least some of the mesocarnivore’s prey. Red rock crab abundance increased significantly over the course of the month-long large carnivore playbacks (Supplementary Fig. 1; Supplementary Discussion), which could only be due to a behavioural change in habitat use, as reproduction in this species requires at least a year. Red rock crabs occur in large subtidal populations and move into the intertidal to forage, where they are killed and eaten by raccoons, which leave the remains, and thus chemical cues, of dead crabs in the water. Surviving red rock crabs may modify their habitat use in response to these chemical cues, as has been demonstrated experimentally in other crab species. The fear cascade evident from the increased abundance of red rock crabs may therefore have resulted from straightforward mechanisms: increasing the fearfulness of raccoons reduced their foraging (Fig. 2), which presumably led to reduced fearfulness in red rock crabs by decreasing chemical cues in the water, in turn leading to the red rock crabs’ increased use of the intertidal (Supplementary Fig. 1).

The loss of large carnivores from habitats across the globe has been linked to far-reaching ecosystem-level consequences—including biodiversity loss and changes in habitat structure—caused by outbreaks of large herbivores and mesocarnivores. Our results suggest that restoration of these ecosystems will require more than just addressing the overabundance of these middle trophic level species, for example, through hunting or removal programs. Such numerical suppression may only affect a subset of hyper-abundant large herbivore and mesocarnivore populations, while the remaining individuals are free to engage in unrestricted foraging. Effective ecological restoration may depend on re-establishing the fear of large carnivores in these ecosystems, which has the potential to affect entire populations of their prey (rather than just those individuals subject to direct killing or removal), suppressing prey foraging behaviour and thereby mitigating the impacts of overconsumption on lower trophic level species. The potential ecosystem-level benefit of the mere presence of large carnivores, and the “landscape of fear” they produce, should therefore be a central consideration in making informed management decisions regarding large carnivore populations.

Our experimental results support the contention that, when it comes to conserving biodiversity and maintaining healthy ecosystems, fear has its uses. By inspiring fear, the very existence of large carnivores on the landscape, in and of itself, can provide a critical ecosystem service human actions cannot fully replace, making it essential to maintain or restore large carnivores for conservation purposes on this basis alone. Ensuring the continuation of this critical ecosystem service the fear of large carnivores provides requires attenuating our own fear of them, which can be accomplished by promoting tolerance and coexistence with large carnivores as an accompaniment to other programs to reduce human-large carnivore conflicts.

**Methods**

**Study area.** Vegetation in the Gulf Islands falls within the Coastal Douglas Fir (Pseudotsuga menziesii) biogeoclimatic zone, and the region experiences a mild Mediterranean climate. This work was conducted on four Gulf Islands. Coal Island (140 ha; 48° 41’ 03” N, 123° 22’ 32” W) is a single-owner private island consisting of ~78% forest, Portland Island (223 ha; 48° 43’ 33” N, 123° 22’ 20” W) and Wallace Island (87 ha; 48° 56’ 34” N, 123° 33’ 04” W) are both fully forested parkland, being entirely within the Gulf Islands National Park Reserve (Portland), or mostly BC Provincial Park (Wallace, 83% of land area). Penelakut Island (954 ha; 48° 57’ 30” N, 123° 38’ 34” W) is the traditional territory of the Penelakut First Nation and home to ~350 people, all residing in a small village on the north end of the island. The majority of Penelakut Island (~86%) is forested. Domestic dogs were present on all Gulf Islands on which this study was conducted, either as the pets of permanent residents (Coal and Penelakut Islands) or accompanying
park visitors (Portland and Wallace Islands), though study sites were chosen well away from areas of high human and dog use to minimize interference.

**Motivation and objectives.** We experimentally manipulated the fear of large carnivores over 2 years and at multiple sites in the Gulf Islands, achieving both temporal and spatial replication of our results. In 2013, we tested the immediate reaction of raccoons to 10 s playbacks of large carnivore vocalizations on Coal, Portland and Wallace Islands. We then used month-long playbacks of large carnivore vocalizations to test for long-term behavioural responses by raccoons and cascading effects on marine biota, on Coal Island in 2013 and on Penelakut Island in 2014. To test whether the fear of large carnivores over 2 years and at multiple sites in the Gulf Islands raccoons are certain to be as familiar with pinnipeds as with dog vocalizations. Most importantly, pinnipeds represent no threat to raccoons, and analysis of the noise data for the presence of raccoons or raccoon vocalizations, we found that there was no difference between pinniped playbacks and silence with respect to raccoon impacts on marine prey (Supplementary Discussion). Sound files were acquired from online audio and video databases, and library archives. In testing the immediate reaction of raccoons to large carnivore vocalizations, we used multiple 10 s exemplars of predator and non-predator vocalizations (10 dog and 5 pinniped), and matched the temporal properties (duration, attack and number of staccato elements) of these two groups of playbacks by visually inspecting the spectrograms and waveforms of all exemplars. We ensured that there were no differences in overall frequency characteristics between the two groups using t-tests to compare each of four frequency characteristics: peak frequency: $f_{peak} = 0.003$, $P = 0.973$; minimum: $f_{min} = 1.46$, $P = 0.180$; maximum: $f_{max} = 0.63$, $P = 0.551$; range: $f_{range} = 0.62$, $P = 0.556$; (5) (non-predator) for all tests). We broadcast 10 s calls at a mean (+ s.d.) volume of 78.0 ($\pm 2.1$) dB at 1 m, with no difference in volume between predator and non-predator vocalizations ($t_{11,13} = -1.3, P = 0.234; n = 10 and 5$). All playbacks were broadcast using identical speakers (Nexxtex Mini Cine 2.0) and mp3 players (Coby Electronics MP301).

To test the long-term response of both raccoons and the nearshore marine community to the fear of large carnivores, we again used playbacks of dog (predator) and pinniped (non-predator) vocalizations. We composed playlists using multiple exemplars of both call types (n = 11 predator and n = 9 non-predator exemplars) ranging in duration from 8 to 79 s, with no difference in duration between the two treatments (mean ± s.d.: 34.1 ± 20.6 s; non-predator: 26.5 ± 18.3 s; $t_{11,13} = 0.84, P = 0.412$). These two sets of playbacks were again matched for temporal properties using visual inspection of spectrograms and waveforms, and we found differences in duration and frequency characteristics between predator and non-predator playlists (peak frequency: $f_{peak} = 0.003$, $P = 0.973$; minimum: $f_{min} = 1.44$, $P = 0.180$; maximum: $f_{max} = 0.63$, $P = 0.459$; range: $f_{range} = 0.86$, $P = 0.400$; (10) (predator) and 9 (non-predator) for all tests). All calls were broadcast at a mean (+ s.d.) volume of 86.1 ($\pm 2.9$) dB at 1 m, with no difference in volume between predator and non-predator vocalizations ($t_{11,13} = -0.13, P = 0.895; n = 11 and 9$). All playbacks were broadcast using identical speakers (Nexxtex Mini Cine 2.0) and mp3 players (The Source HeadRush 2GB mp3 player).

**Raccoon immediate reaction to large carnivore vocalizations.** All 10 s playbacks were conducted by two researchers (J.P.S. and D.R.) between 15 May and 16 September 2013. We located diurnally active raccoons foraging in the intertidal and broadcast at a distance of 5–30 m from the nearest raccoon or non-predator vocalization. We deployed speakers in broadcast at an average (± s.d.) distance of 35 ± 16 m, and the distance between the speaker and the focal animal did not differ between predator and non-predator treatments (one-way analysis of variance (ANOVA); $F_{1,20} = 0.96$, $P = 0.33; n = 45$ (predator) and 27 (non-predator)). Habitat variables that could potentially impact the raccoon during the playback—such as wind speed and the wind direction—were recorded on the video camera at one in the end of the 200 m treatment area. These custom-built speaker systems used identical components to those described above, but were modified to incorporate a motion sensor, which activated a 10 s playback (using the same sets of calls described above) when triggered by a raccoon passing within ~5 m of the sensor. This technique was always active, but remained silent unless triggered. There is no evidence that the minor methodological differences in fear manipulation between the 2 years of the experiment had any effect on our results. Indeed, the effect size on subtidal red rock crab abundance was identical in both years (Supplementary Discussion).

We measured the long-term effects of the fear of large carnivores on several aspects of raccoon foraging on Coal Island in 2013 and Penelakut Island in 2014. We used a network of cameras deployed at each treatment site. Two colour/infrared video surveillance cameras (Spectro Technologies HT7915DNV Bullet Cameras), recording to custom-
Measuring cascading effects of fear. In 2013, we used standard quadrat sampling methods to test whether our month-long playback manipulations affected the abundance of raccoon intertidal prey. On the basis of previous work29 and direct observations of raccoon foraging, our a priori prediction was that our fear manipulations would affect the abundances of small (< 5 cm carapace width) intertidal crabs (non-predatory crabs (Hemigrapsus orogeneticus, H. nasus), black-clawed crabs (Lophopanopeus belius), porcelain crabs (Petrolisthes spp.) and juvenile northern kelp crabs (Pugettia producta)), intertidal fish (pricklebacks (family Stichaeidae) and northern clingfish (Gobiosox maeandricus)), and polychaete worms (families Terebellidae, Orbiniidae, Nereidae and Glyceridae). Following methods described in Suraci et al.29, we quantified species abundance in 0.25 × 0.25 m quadrats at each treatment site on Coal Island at the end of each 28-day treatment period.

To test whether our playback manipulations affected red rock crab abundance, we trapped crabs across 200-m sections of shoreline centred at each treatment site by setting five collapsible mesh crab traps per site just below the low water intertidal zone spaced 50 m apart and left in place for 24 h (ref. 22). On Coal Island in 2013, crab traps were set at the end of each month-long treatment period. Sampling effort was intensified on Penelakut Island in 2014 such that crab trapping was conducted once before the application of any playback treatments (on 11 June 2014) to establish a pretreatment baseline crab abundance, and then at the end of each 28-day treatment period (that is, four times per treatment period). In both years, trap locations remained constant across all trapping sessions at a given site. The effects of the fear of large carnivores may extend beyond those species directly subject to raccoon predation to affect the competitors and prey of the raccoon. Red rock crabs are major intertidal predators, with many resources under threat from other intertidal predators of similar body size, including staghorn scallops, which are not subject to raccoon predation (Supplementary Discussion). We tested whether our fear manipulation treatments affected staghorn scallop abundance by setting conical fish traps (minnow traps) across both treatment sites on Penelakut Island in 2014. Five traps, spaced 50 m apart and baited with ~100 g of frozen herring, were set in the mid intertidal zone at each site and left in place for 24 h. Traps were deployed three times per 28-day treatment period, once immediately before the start of each treatment period and again at the mid-point and end of each treatment period. The same trap locations were used for all fish trap deployments at both sites.

Red rock crabs are known to affect the abundance of several species of gastropod prey, including periwinkle snails (Supplementary Discussion). We hypothesized that, during predator treatments, reduced raccoon predation on red rock crabs would result in increased red rock crab predation on periwinkle snails relative to non-predator treatments. To test this prediction, we conducted short-term snail mark-recapture experiments nested within our fear manipulation experiment on Penelakut Island in 2014, comparing the proportion of marked snails killed by red rock crabs during predator and non-predator treatments. Periwinkle snails were collected from high intertidal beds of Fucus algae at each site and transported back to the laboratory where they were marked with a small dab of acrylic paint on the apex of the shell, and held overnight in seawater tanks. Following Rochette and Dill22, snails were released the next day at each of four release points (spaced 30 to 50 m apart) within the 200-m treatment area at each site. All release points were located at the same tide level (1.0 m above mean lower low water), and a rockaway from large boulders or crevices. Twenty-five snails were released within a 5-cm radius of each release point during afternoon rising tides when release points were submerged under at least 1.5 m of water. The following morning at low tide, immediately following exposure of the release points, two researchers searched a 4-m radius around each point, recovering marked live snails and the marked apices of crushed snail shells. Red rock crab predation on snails produces a characteristic shell crushing pattern26, allowing one to reliably diagnose snail mortality due to red rock crab predation, and counting only shell apices rather than all crushed shell fragments ensures that each crushed snail is only counted once. For each of the 20 released snails, we estimated the proportion of marked snails surviving red rock crab predation over one tide cycle as the number of live snails recovered divided by the total number of live snails and crushed apices recovered at each release point (the fate of snails not recovered could not be reliably ascribed to red rock crab predation). To minimize potential bias due to low recovery rates, we excluded any crushings for which at least 50% of the 20 released snails were recovered, alive or dead (n = 18 trials). For these trials, the average recovery rate was 71% (range = 50–95%), and did not differ between predator and non-predator treatments (t18 = 0.04, P = 0.97). This snail mark-recapture study was replicated four times on Penelakut Island in 2014, at the mid-point and end of each month-long treatment period, using the same four release points at each site throughout both treatment periods.

Statistical analyses. All model assumptions were checked using statistical tests for normality and homogeneity of variance, and the fit of all models was visually inspected using residual versus fitted value plots and quantile–quantile plots37. Where appropriate, means and s.e.s were calculated on normalized data, and back-transformed to the original scale of the data for presentation in figures. All (Generalized) Linear Mixed Effects Models (LMM) were fit using the ‘lme4’ package in R44.

We used a log-linear analysis to test whether playback treatment affected the proportion of trials in which the focal raccoon fled the intertidal following 10 s of playback delivered in a month-long treatment period using a model that allowed for varying intercepts per treatment × island interaction. Data on both the change in foraging and the change in vigilance exhibited by raccoons that did not flee the intertidal following 10 s of playbacks were Box–Cox transformed and analysed using separate two-way ANOVA models including the main effects of treatment and island, and a treatment × island interaction (Supplementary Table 2).

We estimated the duration of time spent in the intertidal during month-long playback treatments for all independent raccoon occurrences on video surveillance cameras, and then used the median duration per camera night in our analysis. Median duration data were natural-log transformed and analysed using a LMM (Supplementary Table 3). To test for a main effect of time since the start of the treatment period (‘night’, measured in days: 1–28) and an interaction between time since the start of the treatment period and treatment × island interaction. Data on the effect of night and the treatment × night interaction were then analysed using LMM (Supplementary Table 3). The significance of model terms was tested using Likelihood Ratio Tests41. In both behavioural analyses, we tested for main effects of treatment and study site as well as a treatment × site interaction. To test for a main effect of time since the start of the treatment period (‘night’, measured in days: 1–28) and an interaction between time since the start of the treatment period and treatment × island interaction. Data on the effect of night and the treatment × night interaction were then analysed using LMM (Supplementary Table 3). The significance of model terms was tested using Likelihood Ratio Tests41. In both behavioural analyses, we tested for main effects of treatment and study site as well as a treatment × site interaction.
and end of each treatment period from the number caught in the same trap immediately before that treatment period. These data were analysed using LMM, including trap location (constant across sampling events) as a random effect. We tested for the main effects of treatment and site, and a treatment × site interaction (Supplementary Table 6).

The effect of our playback treatments on the proportion of marked periwinkle snails escaping crab predation was determined by scoring all surviving snails as 1 and all crushed snails as 0 in each trial of the mark-recapture experiment, and analysing these data using GLMM with a binomial error distribution. There was no evidence for overdispersion in these data (ratio of null to residual deviance = 1.10). Snail release point (constant across all trials at a given site) was included as a random effect. We again tested for the main effects of treatment and site, and a treatment × site interaction (Supplementary Table 6).

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Author contributions

All authors originally conceived of the study, and J.P.S. and D.R. conducted the fieldwork, with the assistance of M.C. and L.Y.Z. J.P.S. and M.C. performed the data analysis and drafted the manuscript. All authors discussed the results and commented on the manuscript.

Additional information

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