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Original Article

Mesopredators retain their fear of humans across a development gradient

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Anthropogenic impacts on wildlife behavior arise both from the immediate presence of people, which induces fear responses in many species, and the human footprint (i.e., landscape modification such as residential development), which affects animal movement and habitat use. Where both disturbance types co-occur, disentangling their impacts remains a challenge. Disturbance effects may interact such that species respond to increased human footprint by either reducing (habituation) or increasing (sensitization) avoidance of human presence. We experimentally manipulated perceived human presence, using playbacks of people talking, across a gradient of human footprint in California's Santa Cruz Mountains and used camera traps to quantify the behavioral responses of bobcats (*Lynx rufus*), striped skunks (*Mephitis mephitis*), and Virginia opossums (*Didelphis virginiana*), mesopredators known to exhibit strong fear response to human presence but which vary in their use of developed areas. Bobcats and skunks reduced activity in response to human playbacks but showed no change in responsiveness to playbacks across the gradient of human footprint, suggesting that these species are similarly fearful of humans at all development levels tested. Opossums exhibited a significant interaction between human footprint and playback treatment such that reductions in activity level in response to human playbacks were strongest at higher levels of building density. Our results indicate that, rather than habituating to human presence, some mesopredators retain a strong fear of humans or become more fearful when inhabiting more developed areas. We suggest that consistently high responsiveness to immediate human presence may benefit mesopredators living in human-dominated landscapes by mitigating the risk of anthropogenic mortality.

Key words: **camera trap, ecology of fear, habituation, human footprint, human impact, playback experiment, sensitization.**

INTRODUCTION

Human disturbance alters the behavior of wildlife, impacting species across taxa and habitat types (Déaux et al. 2018; Tsunoda et al. 2018; Sévêque et al. 2020). Disturbances in varying forms, from human footprint (e.g., landscape modification through development) to human presence (e.g., recreation, hunting), represent distinct stressors with differential impacts on wildlife behavior (Suraci et al. 2021). Many wildlife species alter their behavior in areas of high human footprint, including changing their habitat use and movement across the landscape (Wilmers et al. 2013; Tucker et al. 2018; Suraci et al. 2020; Doherty et al. 2021). Although less is known about the ecological impacts of human presence, its relevance is increasing as outdoor recreation expands and draws more people into remote areas of low human footprint (Cordell et al. 2008). Although often classed together as human disturbance, human footprint and human presence have non-equivalent and at times opposite effects on the behavior of wildlife species (Nickel et al. 2020). Disentangling the effects of human footprint and human presence on wildlife remains a key challenge in conservation. However, an experimental approach to resolving this issue has yet to be applied.

Humans are a major source of mortality for many wildlife species (Darimont et al. 2015), particularly large and medium-sized predators (Persson et al. 2009; Temple et al. 2010; Newby et al. 2013; Wynn-Grant et al. 2018), leading many predator populations to develop strong fear responses to the presence of people (Suraci, Clinchy, et al. 2019; Suraci, Smith, et al. 2019). Fear of humans has been shown to alter foraging behavior in predators, driving changes in hunting strategies and reductions in feeding time (Smith et al. 2017; Lodberg-Holm et al. 2019; Suraci, Clinchy, et al. 2019; Suraci, Smith, et al. 2019). Predator species have also been shown to reduce their overall activity level or to shift their diel activity in order to avoid human disturbance (Wang et al. 2017; Gaynor

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et al. 2018; Tsunoda et al. 2018; Tucker et al. 2018; Ordiz et al. 2019; Suraci, Clinchy, et al. 2019; Nickel et al. 2020). These fear responses can have non-lethal consequences including heightened physiological stress, increased energetic costs, and reduced reproductive success (Smith et al. 2015; Støen et al. 2015; Gaynor et al. 2018, Nickel et al. 2020).

Although many mesopredator species experience heightened mortality in areas of high human footprint (Hill et al. 2019), some species are positively associated with human infrastructure (Randa et al. 2006; Dellinger et al. 2013; Johnson et al. 2015; Moss et al. 2016; Magle et al. 2019). The opportunity to exploit resource subsidies represents a significant benefit that may draw predators into human-dominated landscapes (Bateman and Fleming 2012; Newsome and Van Eeden 2017; Déaux et al. 2018). Another benefit of utilizing highly developed areas for mesopredators is reduced risk of predation and/or competition from dominant predators (Muhly et al. 2001; Berger 2007; Gosselink et al. 2007; Moll et al. 2018). The tension between the risks and benefits of living in a human-dominated environment may be reflected in how predator species react to direct human presence versus how they navigate areas of high human footprint.

Although human presence and human footprint have non-equivalent effects on fear responses in wildlife (Nickel et al. 2020), the two variables may interact. Background levels of exposure to human footprint may modulate a populations' fear response to immediate human presence in ways that facilitate mesopredators exploiting developed areas by either minimizing the lethal threat of a human encounter (i.e., through sensitization) or reducing the non-lethal effects of fear (i.e., through habituation). Sensitization, or increased responsiveness to a stimulus with increased exposure, helps animals avoid costly or lethal encounters (Blumstein et al. 2016). In contrast, habituation, or a decreased responsiveness to a stimulus with increased exposure, mitigates energy spent reacting to benign stimuli (Rankin et al. 2009; Blumstein et al. 2016). In areas of heightened human footprint, predator species may either sensitize or habituate to human presence. If predators sensitize to human presence, they may avoid areas of high human footprint altogether or rely on reactive responses to human cues while exploiting anthropogenic resources (Woodroffe 2011; Valeix et al. 2012; Broekhuis et al. 2013; Lamb et al. 2020). If predators habituate to human presence, they may reduce the time and energy spent on costly antipredator behaviors but may be more likely to experience direct or incidental mortality from humans (e.g., predator control and vehicle strikes) in areas with high human footprint (Wheat and Wilmers 2016; Wynn-Grant et al. 2018; Shimozuru et al. 2020).

The Santa Cruz Mountains in coastal California is an ideal place to disentangle the impacts of human presence and human footprint on wildlife behavior. The area is characterized by high quality wildlife habitat, interspersed with a strong gradient of residential development from rural/exurban to urban centers (Suraci et al. 2020). Even in less populated areas, there is still exposure to human presence, as outdoor recreation is prevalent throughout the region (Nickel et al. 2020). The area is home to several mammalian mesopredators (Wang et al. 2015) including bobcats (*Lynx rufus*) and striped skunks (*Mephitis mephitis*), as well as an omnivorous marsupial, the Virginia opossum (*Didelphis virginianus*). In the Santa Cruz Mountains, these three predator species have been shown to be fearful of humans while also utilizing human-dominated landscapes to varying extents. In this system, bobcats become more nocturnal with increasing exposure to both human presence and footprint (Wang et al. 2015, Suraci, Clinchy, et al. 2019, Nickel et al. 2020), yet bobcat presence is positively associated with human presence on recreational trails (Nickel et al. 2020). Striped skunk occupancy increases with human footprint, but they reduce their activity in response to human presence (Wang et al. 2015, Suraci, Clinchy, et al. 2019; Nickel et al. 2020). Similarly, opossum presence and human footprint have a positive relationship in the region, but opossums reduce their foraging effort in response to human presence (Suraci, Clinchy, et al. 2019; Nickel et al. 2020).

Although observational studies have revealed that the effects of human footprint and human presence are non-equivalent, experiments are needed to tease out their separate effects. Experiments conducted with camera traps in particular can be used to examine the relationship between predator responses to cues and environmental context (Smith et al. 2020). Here, we describe an experimental approach to disentangle the effects of human footprint, human presence, and the interaction between the two on mesopredators in the Santa Cruz Mountains. Specifically, we employed a playback experiment with camera traps to examine behavioral responses of bobcats, striped skunks, and Virginia opossums to simulated human presence across a gradient of background human footprint (i.e., protected areas to suburban development). We investigated three alternative hypotheses regarding the interaction between human footprint and human presence:

1. Sensitization: Mesopredators exhibit stronger avoidance responses to perceived human presence in areas with a relatively high human footprint.
2. Habituation: Mesopredators exhibit weaker avoidance responses to perceived human presence in areas with a relatively high human footprint.
3. No relationship: Mesopredators exhibit the same magnitude of avoidance response to perceived human presence, regardless of human footprint.

METHODS

We conducted this study at sites that spanned a gradient of human footprint throughout the Santa Cruz Mountains (SCM). The SCM is a mixed landscape of coast redwood (*Sequoia sempervirens*) and Douglas fir (*Pseudotsuga menziesii*) forests, open areas of grasslands, live oak (*Quercus* spp.) savannah, and coastal scrub, intermixed with rural, exurban, and suburban development (Suraci et al. 2020). The area is bordered by the cities of San Jose and Santa Cruz. Recent work in the SCM has indicated that the intensity of human presence remains high even in remote, protected areas, due to widespread recreation (Nickel et al. 2020).

We ran a playback experiment at 13 sites throughout the Santa Cruz Mountains between 7 October and 4 December 2019. These 13 sites spanned a total area of 400 km^2 with a minimum separation of 1 km between neighboring sites (Figure 1). We chose playback sites that spanned a gradient of human footprint ranging from remote protected areas to suburban developments. Human footprint at each playback site was estimated as the number of buildings within a 500-m radius of the playback location (i.e., location of speaker and camera, see below), quantified using the Microsoft Maps building footprints layer (https://www.microsoft.com/en-us/maps/building-footprints). Building density ranged from 0 to 391 buildings within 500 m (Figure 1). We defined sites as 500-m radius circles (0.79 km^2 area) around each playback location to match the approximate space use of our three focal species and thus the housing densities that any individual visiting a playback location was likely to have recently experienced. Striped skunks notably

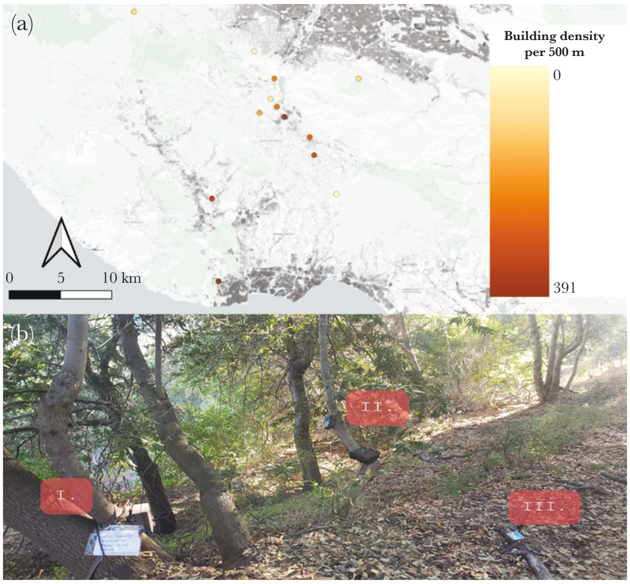

Figure 1
(a) Study area showing the building density associated with each of the 13 playback sites in the Santa Cruz Mountains, CA. Playback sites are color-coded by building density ranging from 0 buildings (light yellow) to 391 buildings (dark orange) within a 500-m radius of the playback location. Building points are shown in black. (b) Field experiment setup at one of the 13 study sites showing (I) motion sensitive wildlife camera, (II) speaker broadcasting control (frog) or human treatments (III) bait and scent lure.

decrease their home ranges through the months of September and February, with home range estimates during these months of 0.7 km^2 for males and 0.4 km^2 for females (Weissinger et al. 2009). Mean opossum home ranges are 1.13 km^2 for males and 0.9 km^2 for females (Ryser 1995). Although mean bobcat home ranges were reported at about 8.89 km^2, a study in southern California found their mean core-use areas to be 1.31 km^2 (Lyren and Crooks, 2009). Defining sites as 500-m radius also ensured no overlap in housing density estimates between neighboring sites.

We acknowledge that building density may in some cases be an incomplete proxy for the human footprint, for instance, in areas with a mix of residential and industrial development, where the level of landscape modification associated with a single industrial building is substantially higher than that associated with a single residential building. However, in the study system considered here (i.e., rural to suburban areas of the Santa Cruz Mountains), development is almost entirely residential. Building density thus provides a useful estimate of human footprint in this system and one that has frequently been shown to affect animal movement and habitat use (e.g., Wilmers et al. 2013; Wang et al. 2015; Nickel et al. 2020, 2021).

We manipulated human presence following the protocol similar to that described by Suraci, Clinchy, et al. (2019). At each site, we deployed a single battery-powered speaker broadcasting either human or control vocalizations. Human playbacks consisted of a single female or male voice reading passages or responding to interview questions. As a control, we used Pacific treefrog (*Pseudacris regilla)* vocalizations since this species is found throughout the Santa Cruz Mountains, does not pose a threat or represent a food source to any of our focal species, and can commonly be heard during day and night (Smith et al. 2017; Suraci, Clinchy, et al. 2019; Suraci, Smith, et al. 2019). We used ten exemplars of each playback type, ranging in duration between 34 and 229 s. Playbacks were broadcast in random order at a consistent volume of 75 dB. Speakers were continuously active, but only intermittently broadcast either human or control vocalizations with each vocalization followed by a period of silence (ranging from 51 to 334 s long) such that speakers were broadcasting 40% of the time and silent 60% of the time. Each experimental replicate ran simultaneously for 8 weeks at each site. We utilized a repeated-measures design such that each site received either human or control playbacks for 4 consecutive weeks followed by the opposite treatment for a subsequent 4 weeks (Suraci et al. 2016; Suraci, Clincy, et al 2019). We randomly selected half of the sites to begin with the control treatment and half to begin with the human treatment. Each site was checked once a week to ensure that playback equipment was functioning properly.

At each playback site, we deployed a motion-sensitive wildlife camera (Bushnell Trophy Cam; Bushnell Corp., Overland Park, KS). The cameras were programmed to take a burst of three photographs when triggered by motion with a 1-min delay between bursts. The cameras were active for the full 8 weeks of the experiment. We placed a scent lure (perforated sardine tin) and food bait (boiled chicken egg) at each site (Figure 1) to increase the chance that an individual of any species would investigate the site and be captured on camera (Suraci, Clinchy, et al. 2019). Lures and baits were replaced weekly. All playback images were scored for the presence of mesopredators by at least two trained individuals, with species assignment based on consensus between independent scorers. We defined an independent predator detection as an image or group of images of a particular species that was separated from another detection of the same species on the same camera by at least 30 min.

To test the effects of human presence and human footprint on mesopredator activity levels, we quantified the number of detections per week of each species at each camera site (Moll et al. 2018; Suraci, Clinchy, et al. 2019). Because experiments were run for 8 weeks, we derived eight activity level estimates for each camera site (four during the human treatment and four during the control treatment), with the exception of a single site for which camera failure resulted in only 7 weeks of data (four human and three control). A detection event is the result of two processes: 1) whether a species is present in the vicinity of a camera site and thus available to be sampled (a binary process); and 2) the species activity level at a camera site if present, which determines the number of times the species is detected (a Poisson process) (Moll et al. 2018; Suraci, Clinchy, et al. 2019). We therefore fit zero-inflated Poisson (ZIP) (Zuur et al. 2009) models to predator detection data, which can capture both processes through 1) a binomial component modeling whether each detection estimate is a zero and 2) a Poisson component modeling the number of detections per week (a proxy for activity level). Model covariates included playback treatment, building density, and the number of detections of other mesopredator species per week (e.g., for models of striped skunk activity level, the number of bobcat and opossum detections in each week). We included the latter term to account for the potential effects of competition with (or facilitation by) other mesopredator species (Prugh and Sivy, 2020). In all models, we fit random intercepts for camera site on both the binomial and Poisson submodels to account for repeated measurements of predator activity level at each site. For each focal species (striped skunks, bobcats, and opossums), we fit a full ZIP model consisting of 1) covariates for building density and detections of other mesopredators on the binomial (i.e., zero or nonzero) component to control for the potential influences of both development and interspecific interactions on whether a given mesopredator was available to be sampled, and 2) covariates for playback treatment, building density, other mesopredators, and the interaction between playback treatment and building density on the Poisson component (i.e., number of detections per week). For each species, we also fit a reduced model with the playback treatment x building density interaction removed. For species for which the playback treatment x building density interaction term was not significant in the full model (i.e., 95% credible intervals crossed zero), we interpret the results from the no-interaction model. All models were fit in a Bayesian framework using the Stan programming language called through R via the rstan package (Stan Development Team, 2020). For each model, we ran 5000 iterations of three Hamiltonian Monte Carlo chains retaining 1000 samples from the posterior distribution of each chain. We used vague priors for all variables and random starting points for all chains. We checked model convergence by visually inspecting trace plots and confirming that the Gelman–Rubin statistic ("R-hat") was < 1 for all parameters. We tested model fit to the data using Bayesian *P*-values, which compare statistics calculated from model-generated data with those calculated from observed data. A well-fitting model will have Bayesian *P*-values near 0.5, indicating that model predictions are equally likely to be higher or lower than observed data. *P*-values > 0.95 or < 0.05 indicate poor fit (Hobbs and Hooten 2015). Here, we calculated Bayesian *P*-values for the mean and skew of model-generated and observed data (Hobbs and Hooten 2015).

RESULTS

Bayesian *P*-values indicated that all ZIP models fit the data well ($0.42 \leq P \leq 0.65$ for all models). The human playback treatment had a negative effect on activity level of both striped skunks (playback treatment coefficient estimate [95% CI] = −0.52 [−1.04 to −0.01]) and bobcats (−1.56 [−2.86 to −0.42]; Figure 2a and b), leading to 40% and 79% reductions, respectively, in the number of skunk and bobcat detections per week relative to the control treatment (Figure 3a and b). However, neither striped skunks nor bobcats exhibited a significant response to increasing building density (striped skunk: −1.90 [−7.44 to 4.34]; bobcat: −0.62 [−5.13 to 4.18]) or an interaction between playback treatment and building density (striped skunk: 0.74 [−2.88 to 4.18]; bobcat: 2.94 [−1.48 to 8.19]; Figure 2a and b), indicating that their responses to perceived human presence were consistent across the gradient of human footprint. Opossums exhibited a significant negative interaction between playback treatment and building density (coefficient estimate = −1.37 [−2.41 to −0.33]; Figure 2c), indicating that opossums only reduce their activity levels in response to perceived human presence at higher levels of human footprint. Indeed, although error around model estimates was substantial, our ZIP model predicted that the effect of human presence on opossum activity only becomes negative (relative to controls) at building densities greater than 60 buildings within a 500-m radius (exurban housing density; Theobald 2005) (Figure 3c). No mesopredator exhibited a response to the detection rate of other mesopredators at the camera site (all 95% CIs crossed zero, Figure 2).

DISCUSSION

Our study examined the relative importance of human footprint, human presence, and their interaction on animal responses to human disturbance. Past observational studies have demonstrated that human footprint and human presence have separate and at times contrasting effects on wildlife behavior (Nickel et al. 2020). By utilizing a playback approach, we were able to experimentally isolate human presence from human footprint, thus allowing us to disentangle the effects of these two types of human disturbance. We found that all three predator species reduced their activity levels in response to perceived human presence, with striped skunks and bobcats showing no change in the intensity of their fear response to human presence across the human footprint gradient, consistent with Hypothesis 3 above. Opossums exhibited a stronger fear response to human presence at higher background levels of human footprint, consistent with Hypothesis 1 and indicative of sensitization to perceived risk from humans. Importantly, we found no evidence for habituation to human disturbance (i.e., Hypothesis 2) for any of the focal predators, suggesting that, even for highly human-associated species like skunks and opossums, fear of humans may not attenuate with increasing human footprint.

Our results support previous work in the SCM which demonstrated that predators reduce their activity levels when exposed

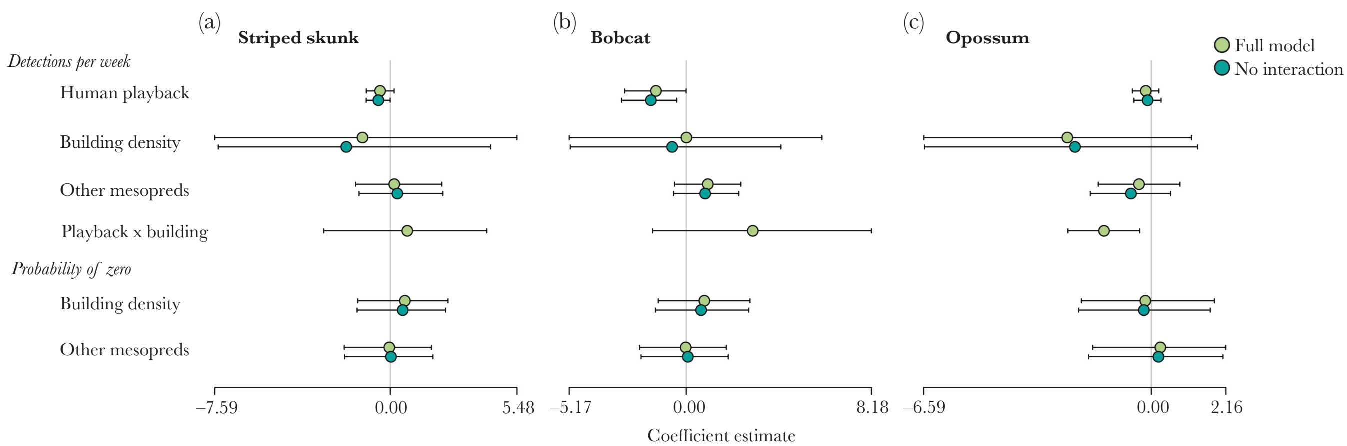

Figure 2

Coefficient estimates and 95% Bayesian credible intervals for zero-inflated Poisson models testing the effects of perceived human presence and building density on medium-sized mammalian predator activity. Results of the full models (i.e., including human playback by building density interactions, green symbols) and no-interaction models (blue symbols) are shown for (a) striped skunks, (b) bobcats, and (c) Virginia opossums.

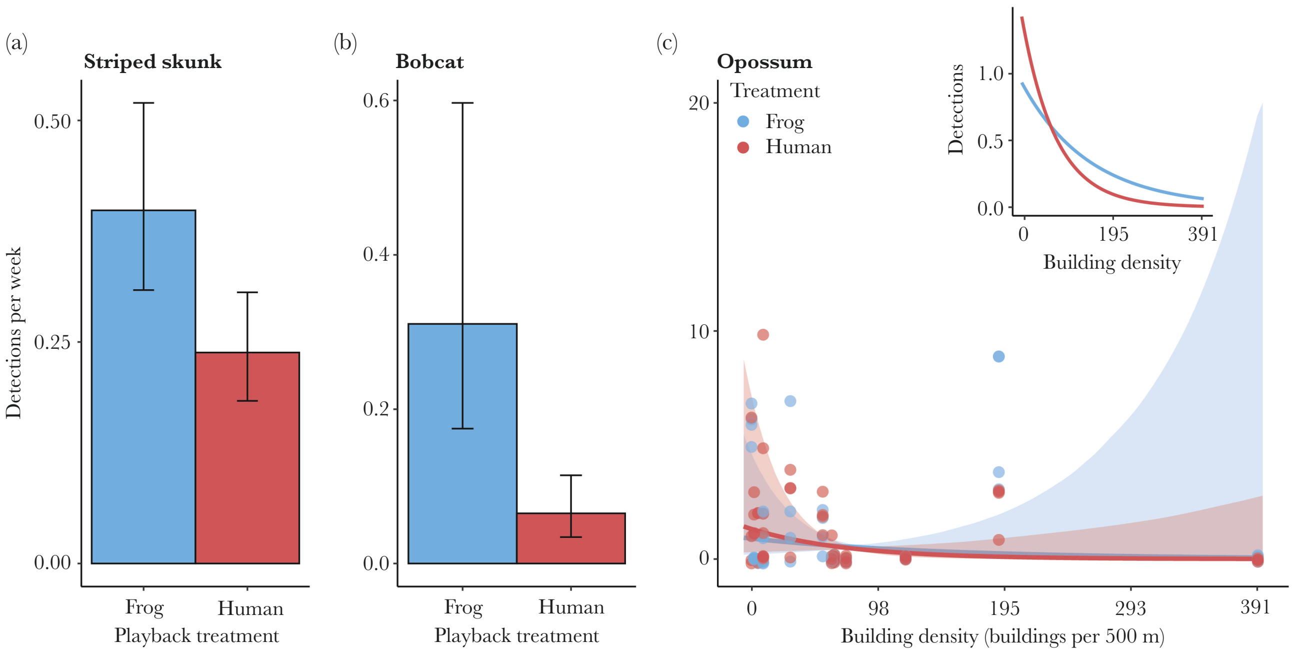

Figure 3
Shifts in mesopredator activity levels in response to human disturbance. Bar plots show reductions in detections per week of both (a) striped skunks and (b) bobcats in response to human playbacks, relative to controls. Error bars are 95% Bayesian Credible Intervals (CI) around predicted average detections per week, derived from Zero Inflated Poisson (ZIP) models. (c) Interaction between playback treatment and building density in their effect on Virginia opossum activity level. Points are number of detections per week for each week of the playback experiment at each camera site across the building density gradient. Lines are the predicted average detections per week (along with 95% CI) across the building density gradient during the human (red) and frog (blue) playback treatments, as determined by ZIP models. The inset in (c) shows the ZIP prediction lines in greater detail.

to human presence in remote areas (Suraci, Clinchy, et al. 2019). Here, we demonstrate that these behavioral impacts occur across the human footprint gradient, including in exurban and suburban areas. We found no evidence of habituation among the focal species in this study, instead demonstrating that predator responsiveness to humans either remains consistent or increases with increasing disturbance associated with landscape modification. Opossums were the only species for which we detected a change in responsiveness to human presence across the gradient of human footprint, with this species exhibiting a greater reduction in activity level in response to human playbacks at building densities above 60 houses per 500 m. This difference between species may reflect actual differences in perceived risk from humans, or may have been driven in part by the fact that opossums were detected at higher building densities than were the other two study species. Opossums frequently occurred at our suburban study site with the second highest building density (191 houses per 500 m), whereas the other two species were not detected at building densities higher than 119 houses per 500 m. Opossums may have a higher underlying tolerance of human-dominated landscapes, which could explain their presence at sites with higher building densities. A study on anthropogenic disturbance in San Diego County, CA found that Virginia opossums in their study area preferred areas characterized by intensive development (Markovchick-Nicholls et al. 2008). Opossum exploitation of more intensively developed areas may necessitate their stronger avoidance of immediate human presence to avoid conflict with humans, leading to sensitization.

Past observation work in our study area using large (≥50) camera trap arrays has also demonstrated predator response to residential development. In these past studies, bobcat detections tended to decrease and skunk and opossum detections tended to increase with increased building density (Wang et al. 2015; Nickel et al. 2020). Despite covering a comparable human footprint gradient, we did not detect similar responses to building density alone in the present study. This is likely due to methodological differences—our experimental approach examined whether changes in behavioral responses to human presence differed based on underlying differences in human footprint but provided less statistical power than large scale camera trap grids to detect responses to the building density gradient itself. Additionally, our study used baited camera sites to increase the capture frequency of mesopredators (du Preez et al. 2014; Mills et al. 2019), whereas camera sites in Wang et al. (2015) and Nickel et al. (2020) were unbaited. However, this difference in methodology is unlikely to have affected our ability to detect species responses to housing density as all three of the focal mesopredator species are known to be attracted to the bait types used (Suraci, Clinchy, et al. 2019) and are thus unlikely to have avoided baited camera sites if present.

There are significant costs associated with over-and under-responding to risk from human presence (Smith et al. 2021). If sensitization results in over-responding to threat, the animal is subject to the sub-lethal costs of fear such as decreased energy intake, increased energetic costs, and reduced reproductive success (Williams et al. 2006; French et al. 2011; Zanette et al. 2011; Smith et al. 2015; Wang et al. 2017, Doherty et al. 2021; Nickel et al. 2021). However, if habituation to human presence results in under responding to threat, then the outcome can be lethal (Mattson et al. 1992; Kloppers et al. 2005). A potential explanation for why even highly human-associated species may fail to habituate to humans is that not habituating enables species to avoid human-caused mortality while still exploiting anthropogenic resources. If habituated to humans, wildlife may act more boldly, potentially taking resources in plain sight (Déaux et al., 2017) or engaging in other behaviors that expose them to direct risk from humans. This in turn can lead to increased human-wildlife conflict and increased likelihood of fatality or depredation for the wildlife species (Denkinger et al., 2013; Wheat and Wilmers 2016; Newsome et al., 2017). By maintaining fear of humans, wildlife may be more likely to avoid human presence before direct conflict arises. In this sense, not habituating may be preferable to habituating when it comes to ensuring long-term access to resources. Additionally, retaining a consistent fear response to humans, rather than sensitizing to human cues, may be beneficial if animals are still able to spend time foraging in human-dominated landscapes without avoiding these areas altogether or wasting energy by fleeing from non-lethal stimuli. Mesopredators are increasingly using human-modified landscapes for various reasons such as resources and safety from predators (Gosselink et al. 2007; Fedriani et al. 2008; Newsome and Van Eeden 2017). We suggest that retaining fear of humans even in urbanized environments may support coexistence in these systems by helping mesopredators avoid sources of anthropogenic mortality.

A meta-analysis of 16 species found that overall mammals in disturbed areas are more tolerant of humans than undisturbed populations (Samia et al. 2015). This may suggest that mammals are likely candidates to habituate to humans. However, tolerance is not always evidence of true habituation, given that individuals may be tolerating human presence because of other factors, such as lack of resources elsewhere (Blumstein 2016). Having evidence of tolerance does allow the chance to assess the possible causes, including that the process of habituation could be underway. In Quebec, Canada, researchers assessed other probable causes of differences in tolerance before concluding that eastern gray squirrels (*Sciurus carolinensis*) were likely habituating to humans (Engelhardt and Weladji 2011). Overall, the consistent response of bobcats and skunks to human presence in our study strongly suggests that the process of habituation has not yet occurred to any substantial degree. Instead, we have evidence that the process of sensitization is potentially underway in the case of the opossum. In addition to tolerance levels, life history traits of mammal species also play a role in differential responses to human disturbance. A study analyzing 24 mammal species from 61 populations throughout North America found that small size, omnivorous diet, low space requirement, and fast breeding were predictors of a positive relationship with human footprint, whereas life history traits were not predictors for response to human presence (Suraci et al. 2021). Although opposing responses to human footprint and human presence among mammals may seem counterintuitive, the mismatch can be explained by various mechanisms, for example, species that have a strong association with human footprint may avoid human presence through being most active at times when less humans are active (Suraci et al. 2021).

Although we find it unlikely that there is species-wide habituation occurring in our study species, there is the possibility of individual habituation. It may be that certain individual opossums, skunks, or bobcats are more adaptable to human presence than their counterparts. Other habituation studies have focused on individuals, such as a study on yellow-eyed penguins (*Megadyptes antipodes*), in southern New Zealand, which found evidence that penguins with calm personality types were more likely to habituate to humans than those with aggressive personality types (Ellenberg et al. 2009). Conversely, an experiment studying eastern chipmunks (*Tamias striatus*) found no evidence of individual variation in habituation (Martin and Réale 2008). This is a relatively new topic of study and further study into individual habituation will be beneficial. It is important to note that habituation in individuals can lead to evolutionary changes over time. For example, evidence suggests that parental habituation in coyotes (*Canis latrans*) leads to a reduced fear response in offspring towards humans (Schell et al. 2018).

There are potential negative fitness consequences associated with long-term human disturbance. Although some species may often navigate modified landscapes with high human activity, it is important to recognize that even these species may be negatively affected by human activity. Here we discovered reduced activity levels as a consequence of fear in mesopredator species, but fear of human presence can additionally be reflected through other behavioral changes such as shifts in diel activity or feeding behavior, and it can be studied through a physiological lens (Støen et al. 2015; Smith et al. 2017; Tsunoda et al. 2018). A recent study on California ground squirrels (*Otospermophilus beecheyi*) in Contra Costa County, CA found that although the squirrels in their human-disturbed study site appeared human-tolerant, they were facing sublethal consequences such as heightened fecal glucocorticoid metabolite levels and lower body masses (Hammond et al. 2019). Similarly, in a human-habituated yellow-bellied marmot *(Marmota flaviventer)* population, individuals in highly disturbed colonies gained less body mass overtime compared to counterparts in areas of less disruption (Uchida and Blumstein 2021).

As human presence and human footprint continue to increase globally, these two forms of disturbance will affect animal behavior in species across taxa and ecosystems. Further study into habituation and sensitization will provide insight into strategies that allow species to navigate life in human-dominated landscapes. Understanding the benefits and risks that individual species face in areas of high human footprint could influence policy-making, such as choosing how to manage food waste or deciding whether and where to implement wildlife crossings. We encourage further adoption of field experiments to disentangle co-occurring human disturbances in order to help conservationists pinpoint strategies for both promoting species survival and mitigating human-wildlife conflict.

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