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LETTER

Habituation and tolerance in coyotes (*Canis latrans*), a flexible urban predator

Emily R. Golden Beam[1] | **Joel Berger**[2,3] | **Stewart W. Breck**[4] | **Christopher J. Schell**[5] | **Joanna E. Lambert**[6]

[1]Department of Environmental Studies, University of Colorado Boulder, Boulder, Colorado, USA

[2]Department of Fish, Wildlife and Conservation Biology, Colorado State University, Fort Collins, Colorado, USA

[3]Wildlife Conservation Society, New York, New York, USA

[4]National Wildlife Research Center, USDA-WS, Fort Collins, Colorado, USA

[5]Department of Environmental Science, Policy, and Management, University of California Berkeley, Berkeley, California, USA

[6]Department of Environmental Studies and Department of Ecology and Evolutionary Biology, University of Colorado Boulder, Boulder, Colorado, USA

Correspondence
Emily R. Golden Beam, Department of Environmental Studies, University of Colorado Boulder, 4001 Discovery Dr, Boulder, CO 80309, USA.
Email: emily.beam@colorado.edu

Funding information
University of Colorado Boulder

Abstract

The behavioral mechanisms by which urban wildlife adapt to urban landscapes and disturbances within these environments are poorly understood. Such understanding can be important for wildlife managers, especially if the species is of concern to human and pet safety, such as the coyote (*Canis latrans*). Here, we evaluate coyote tolerance to the presence of humans, pets, and anthropogenic landscapes, to better understand how coyotes are conditioned to live in urbanizing landscapes. Using continuous focal follow and instantaneous scan sampling, we collected data on metrics of anthropogenic development and coyote flight response. We used cumulative link mixed models to determine that intensity of behavioral response to observation was impacted by habitat, human visitation to sites, and coyote group composition. These data may be useful to managers for profiling potentially problematic individual animals and identifying strategies for human–coyote coexistence.

KEYWORDS

coyote, habituation, tolerance, urban behavior

INTRODUCTION

All wildlife must respond dynamically to novelty to survive and reproduce (Ditchkoff et al., 2006; Fleming & Bateman, 2018; Lambert & Berger, 2022; Rottenborn, 1999). Dynamic response to novel stimuli is facilitated by a complex integration of phenotypic plasticity, learning, and genetics (Gross et al., 2010; Harris & Hofmann, 2014; Sasakura & Mori, 2013). Behavioral flexibility in particular aids rapid response to changing ecological conditions thereby allowing an animal to take advantage of emergent resources. Eventually, if a novel stimulus has no deleterious consequences, behaviorally plastic animals can habituate and become more tolerant (Bejder et al., 2009). Conversely, increased sensitization may occur if the stimulus carries cost to the animal. In urban settings, wildlife interactions with humans and their pets are typically benign to an animal but can also be highly conflictual and require intervention on the part of animal managers. Better understanding of how animals either habituate or become sensitized to anthropogenic stimuli such as the presence of humans and their pets can thus yield important insights for animal management and human-wildlife coexistence.

Coyotes, *Canis latrans*, have experienced rapid range shifts in the last century that have brought this species into urban environments across North America (Bateman &

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Fleming, 2012; Gompper, 2002; Hody & Kays, 2018). Coyotes are successful in human-dominated habitat for diverse reasons including reduced abundance and distribution of apex predators, an expanded feeding niche, and behavioral plasticity (Bateman & Fleming, 2012; Berger, 2010; Crooks & Soulé, 1999; Lowry et al., 2013), rendering them an ideal candidate for exploring behavioral responses to disturbance in anthropogenic landscapes. Additionally, because coyotes can negatively engage with humans and their pets in shared urban spaces (Bateman & Fleming, 2012; Poessel et al., 2013; Timm et al., 2004), knowledge about coyote tolerance could help managers better predict bold, and potentially problematic, behavior and mitigate negative human–coyote encounters.

Understanding how animals habituate requires detailed data on individual and group-level behavior, a challenging undertaking with species that have large home ranges, such as most carnivorans. Indeed, most of the work on urban coyotes has relied on tagging technology for tracking individuals (Breck et al., 2019; Gehrt et al., 2011; Gese et al., 1989; Poessel et al., 2013; Shivik et al., 1997; Thompson et al., 2021; Wurth et al., 2020). While remote telemetry and tagging yields high-quality and fine-grained data on animal movement and ecology, it is costly both in terms of budgets and impact to telemetered animals (Burrows et al., 1994; Hopkins & Milton, 2016). Thus, an ancillary goal of this work was to explore the efficacy of forgoing such technology and methodology and using noninvasive, direct behavioral observational methods for studying wild coyotes in urban landscapes.

Here, we present results from research designed to measure tolerance of urban coyotes to observation given human and dog presence across recreational sites. We centered this effort in the city and county of Broomfield, a suburb within the greater Denver metropolitan area at study sites with documented histories of human–coyote conflict (Bonnell & Breck, 2017; Breck et al., 2019; Poessel et al., 2013). We hypothesized that higher levels of tolerance to human and dog presence would positively co-vary with human visitation rates in urban green spaces.

Practitioner points

- Coyotes in recreational areas are less tolerant of direct observation, so managers could use mowed buffer zones around areas of high human use to promote coexistence in shared urban parks.
- Urban parks that host higher levels of human activity are also home to coyotes that are more tolerant to human observation and may behave more boldly around humans.

METHODS

Sites

We observed coyotes at six sites in Broomfield, Colorado, which is located centrally in the Denver metropolitan area between Boulder and Denver in the American West (39.9205°N, 105.0867°W) (Figure 1). It was founded in 1877 and was originally an agrarian town, but by 2000, the city had expanded to become a county as well. The human population is currently well over 55,000 people, and the city and county cover 8702.4 hectares (City and County of Broomfield, n.d.).

Our six study sites are managed by the Broomfield Open Space and Trails Department and included: Great Western (50.2 ha), Future Reservoir (34.8 ha), Ridgeview (0.87 ha), Metzger Farm (2.01 ha), Broomfield County Commons (2.64 ha), and The Field (1.17 ha). Each site has a history of coyote presence, and some have been the subject of previous coyote research (Bonnell & Breck, 2017; Breck et al., 2019; Grant et al., 2011; Poessel et al., 2013). This research was conducted via trapping and collaring individual coyotes, though there is no evidence that such efforts would have lasting impacts on coyote behavior outside of behavior while trapping and collaring (Breck, personal communication, February 17, 2023). There were also several years in between that work and this effort, which should have allowed for turnover in the coyote population at these sites.

The sites differ along a gradient of human use: two of the six sites, Great Western and Future Reservoir, were closed to the public, while the others were open and regularly experienced recreational visitors.

Study design

Our research methodology was designed to test levels of tolerance and habituation (which has been defined by Blumstein (2016) as an animal's adaptive ability to decrease responsiveness to a "harmless" stimuli) using boldness as an index (Breck et al., 2019). We used boldness as a proxy for tolerance and habituation because as individuals are repeatedly exposed to anthropogenic stimuli that are innocuous, they develop a tolerance to the stimuli. Over time, this individual-level tolerance can build to a population-wide habituation, in which anthropogenic stimuli do not elicit fear responses (Blumstein, 2016; Nisbet, 2000). This may occur due to learning, genetics, or sorting (Breck et al., 2019; Schell et al., 2018), and once habituation happens, studies have found that individuals in habituated populations begin to behave more boldly (Cavalli et al., 2018; Fossett & Hyman, 2021; Uchida & Blumstein, 2021).

We collected observational data on coyotes over a 4-month study season (May–Aug 2019). Field effort was consistent across the six sites such that each site was observed for an equivalent amount of time (80 h). We visited one site a day for either a morning or afternoon session. Morning sessions began 30 min before the sunrise and ran until 1200, and afternoon sessions ran from 1200 until 30 min after sunset, or until it was too dark to see. The lead author (Golden Beam) was assisted in the field by one to three field technicians, depending upon availability. Field technicians were undergraduate students from the University of Colorado-Boulder who had been trained on field methods.

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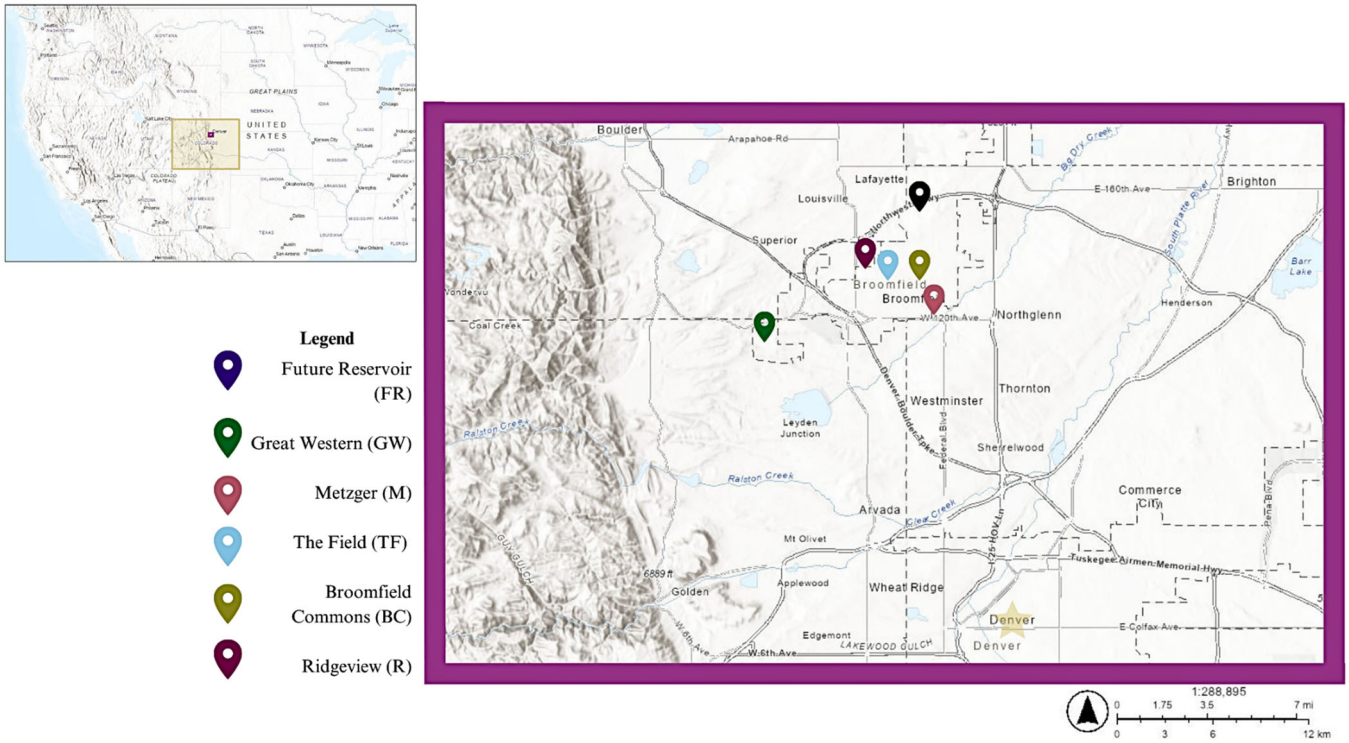


FIGURE 1 Map of field sites in Broomfield, Colorado, USA. Maps made in ArcGis (Esri, 2019).

TABLE 1 Flight behavior categories for urban coyotes based on Breck et al. (2019).

Rank	Description
0	Coyote does not initiate flight behavior.
1	Coyote moves less than 3 m away after observing researcher and stops and looks back in the direction of the stimulus/researcher less than 3 m from the original starting point.
2	Coyote moves more than 3 m away after observing researcher and stops and looks back in the direction of the stimulus/researcher more than 3 m away from the original starting point.
3	Coyote moves away from the area, either quickly or slowly, and looks back while retreating.
4	Coyote flees the area after input. Locomotion involves rapid directed movement. Coyote does not stop or look back as it retreats.

We located and observed coyotes using ×60 scopes and ×10 binoculars. When coyotes were not immediately visible using these methods, we followed social trails (evidence of group movement through the landscape) or observed coyote scat piles and other areas where coyotes frequently spend time—along fence lines, in riparian areas, along man-made two-track roads. Once animals were visible, we took note of their distance from the observer using digital range finders, and their behavioral reaction to observation (Table 1). When multiple coyotes were present, we collected data on group composition (mainly number of individuals, as coyotes are notoriously difficult to sex in situ), selected a focal individual based on which individual was closest and readily visible, and took data on him or her until that animal was no longer visible and no longer easily followed without influencing the animal's behavior. In each case, researchers were the closest human to coyotes (compared to park visitors).

Tolerance in coyotes is operationally defined in terms of flight from stimulus. Thus, though we endeavored to conduct our study to be as minimally invasive as possible, we still had to stimulate coyote behavior in some way. As opposed to approaching animals to stimulate flight (a commonly used tactic; see Blumstein et al., 2003; Breck et al., 2019; Young et al., 2015), when we were in the presence of a coyote, we stared at the animal and measured the individual's flight behavior from the researcher. When researchers located a coyote, they noted when a coyote's head orientation and gaze indicated that the coyote had seen the researcher. We were able to ascertain that the coyotes were responding to researchers specifically by noting the orientation of the head and gaze (pointed at the researcher) and the distance between the coyote and the disturbance (for recorded interactions, researchers were always the closest to the coyote compared to recreational visitors). When there was a direct line of sight to the animal, we took distance data with a rangefinder (Leupold RX-1000i TBR) and noted the coyote's flight behavior, or lack thereof. Flight behavior was recorded following protocol forth by Breck et al. (2019), in which they assessed flight

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TABLE 2 Cumulative link models run to assess coyote flight behavior response with the best-fit model (determined by the lowest AIC and the ANOVA).

Model	Variables	*df*	AIC	ΔAIC	Pr(Chi)
1	Null, no variables		231	-	-
2	Habitat	2	228	−3.00	0.03**
3	Habitat + Group Composition	2	226	−2.00	0.07
3	Habitat + Group Composition + Average Daily Human Presence	1	224	−2.00	0.03**
4	Habitat + Group Composition + Average Daily Presence + Average Daily Dog Presence	1	224	0.00	0.24

Abbreviations: AIC, Akaike Information Criterion; ANOVA, analysis of variance.
**Denotes statistically significant $p < 0.05$.

response from a stimulus (a researcher's approach) along an ordinal scale from 1 to 4, with lower scores associated with bolder, less flight-prone animals and a higher score associated with less bold, more flighty animals (Table 1). This scale was based on methods utilizing collars to locate animals and human approaches to stimulate flight responses to collect flight initiation distance (FID), so we made some modifications to better reflect our noninvasive methodology (i.e., lack of collars relaying animal location information and not directly approaching individuals once located). To minimize disruption to animal behavior, we did not overtly approach our study subjects; instead, we monitored coyotes from where we spotted them. To account for the fact that not all coyotes initiated flight after observing researchers, we added a new category of "no response," creating a scale from 0 to 4 (Table 1). Over the course of the field season, we only collected data in instances in which we were certain that coyotes were responding to research observation, as opposed to other human activity.

Beyond collecting data on individual flight behavior in response to researcher observation, we also collected data on site-level vegetation and recreational patterns. The habitat specific to where an individual coyote was spotted by an observer was collected as a categorical variable—either "general grassland," "riparian," or "recreational zone." Habitat class categories were created after surveying the sites during the pilot stage of the project (spring of 2019) and consulting the city's GIS files and findings (City and County of Broomfield, 2019; Wenk Associates, Inc. et al., 2010). To collect information on recreational uses of the sites and how that may influence coyotes' flight behavior when observed by researchers, we tallied the number of people and the number of dogs at each site per observational bout (a.m. or p.m.). The count data we collected over the field season was then averaged to give us a general understanding of human and dog presence at each of the sites. Additionally, because we visited sites on a randomized schedule, this helped to mediate the large swings in recreational activity across weekdays and weekends.

Lastly, we were interested in exploring whether a noninvasive study without collars or tags could still differentiate among individual coyotes. We attempted to use direct observation to identify individual coyotes. We took notes on physical markings and potentially differentiating behavior.

Statistical analysis

Statistical analyses were performed in R to identify significant anthropogenic and environmental predictors of flight behavior (R Core Team, 2021). To investigate the role of anthropogenic landscapes and recreational use, we investigated three explanatory variables' relationship to our response variable of coyote behavioral response: (i) habitat type, a categorical variable that differed based on where each individual coyote was observed, (ii) daily average human presence, a numeric variable that differed based on which site the coyotes were in, and (iii) daily average dog presence, another numeric variable differed based on site as well. We used a cumulative link ordinal regression model (CLM) with a logit link function that allowed for mixed effects from the package *ordinal* (Christensen, 2015) because of the ordinal nature of the response variable (flight behavior) and because we anticipated needing to use a random effect, or grouping variable, to best explain our data. We explored the impact of site as a potential random effect. To do so, we compared identical models with and without a random effect by utilizing AIC values and conditions of the Hessian values (Christensen, 2022). Once a superior random effect was identified, we generated a variety of models (including a null) and identified a best fit model via AIC values and analyses of variance (Table 2).

To understand the output of the best-fit model, we exponentiated coefficients and calculated 95% confidence intervals in R. We used our best-fit model and the program *sjPlots* to visualize model output (Lüdecke, 2022). Where applicable, graphs were generated with a color-blind-friendly color palette developed by Steenwyk and Rokas (2021).

RESULTS

Observational effort and noninvasive methodology

Over the course of the field season, the research team accrued nearly 10,000 h of joint observational effort resulting in a data set of 97 total individual observations of coyotes. Detection of coyotes was lowest at Great

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Western and Ridgeview (less than a minute of direct observation time at each site) and was highest at Broomfield Commons and The Field (with over 3 and 2 h of coyote observations respectively). This pattern presumably existed due to differences in site area and changes in coyotes' seasonal usage of specific sites. The average duration of coyote observations also followed this pattern, with the lowest average occurring at Great Western and Ridgeview, and the highest occurring at Broomfield Commons and The Field. Most often, coyotes were spotted alone (60.2% of observations), but group size varied from one individual to five individuals. Distance between researchers and coyotes varied from 24 to 240 m, though distance was only able to be recorded for 39 observations (40.2% of observations) due to rapid interactions with the coyotes, or a disrupted line of sight to the coyote that did not allow for accurate rangefinder readings. Therefore, due to a lack of data, distance from the observer was not used as a fixed nor random effect in modeling efforts. Lastly, despite our time in the field, we were unable to predictably differentiate among individuals.

Flight behavior analysis

Across the six sites, the average flight behavior response was 2.2. In sites that were open to the public, the average flight behavior was 2.2 and in sites that were closed to the public the average flight behavior was 2.5. This initially suggests that coyotes in sites that are open to the public have lower, and thus bolder, flight behavior scores on average. However, because so few data points originated from coyotes in closed sites, more data would need to be collected and *t* tests conducted to further explore this.

We determined that adding site as a random effect did improve model fit ($p = 0.001$). In the best-fit model (text box 1), recreational habitats had a positive, significant relationship with behavioral response ($\beta = 1.09 \pm 0.52$, $p < 0.05$, Table 3), average total people in a day had a significant negative relationship with behavioral response ($\beta = -6.25e{-}3 \pm 2.96e{-}3$, $p < 0.05$, Table 3), and groupings of more than two coyotes had a nearly significant negative relationship with behavioral response ($\beta = -1.97 \pm 1.09$, $p = 0.07$, Table 3). Specifically, based on the exponentiated coefficient, this model demonstrates that when all other variables are held constant: for coyotes in recreational habitats, the odds of having a higher, and thus less tolerant, response is nearly two times that of coyotes in the other habitats; for coyotes at sites with higher average human presence, we would expect a 0.623% decrease in the behavioral response score; and, for coyotes in groups larger than two, there is an 88.0% decrease in the odds of a coyote logging a higher behavioral response score. Thus, our model demonstrates that coyotes behave less boldly in recreational habitats and more boldly in sites with more people and when they are in groups of more than two individuals.

We used the model and the *sjPlot* package to generate predicted probability values for behavioral response based on habitat, coyote group composition, and total people (Figures 2 and 3).

TABLE 3 Beta estimates and associated uncertainty for the best-fit model with asterisks denoting statistically significant fixed effects.

Fixed effect	β	SE	Pr(>|z|)
Riparian habitat	−1.21	1.12	0.28
Recreational habitat	1.10	0.52	0.04**
Multiple coyote group	−1.97	1.09	0.07
Pair coyote group	−0.29	0.48	0.54
Total people	−6.25e−3	2.96e−3	0.03**

**Denotes statistically significant $p < 0.05$.

DISCUSSION

The best-fit model found strong support for urban coyotes that have habituated to people in urban parks in Broomfield, Colorado. Our best-fit model illuminated a significant, inverse relationship between the average number of people visiting a site and coyote flight behavior: as more people visited sites, coyotes were more likely to log bolder behavioral scores. Additionally, the predicted probability of a coyote initiating flight due to researcher observation is consistently higher than the predicted probabilities of other, less bold flight responses, no matter what independent variable is being considered (Figures 2 and 3). This is suggestive of increased habituation and tolerance to observation in urban parks, which would be an adaptive strategy to conserve energy and reduce stress in the face of harmless stimuli (Blumstein, 2016). In these urban parks, where legislation protects wildlife from dogs (leash laws) and lethal pressure, humans may be viewed by coyotes as an innocuous presence, and such consistently low-threat stimuli is ideal for yielding tolerance and habituated behavior (Rankin et al., 2009). This may also explain why we were able to observe more coyotes in sites with more recreational zones, as these spaces would support more recreation and thus increased coyote habituation to humans.

In addition to finding evidence of habituation among urban coyotes in Broomfield, Colorado, we also saw a strong influence of site, which we used as a random effect, on coyote behavior ($p = 0.001$). This suggests that site, which in our study may be considered equivalent to pack, has an influence on shaping coyote behavior. This could be due to learning in a highly intelligent, social species (Young et al., 2019); or it could be reflective of genetics and shared landscape-level evolutionary pressures (Wurth, 2018). The influence of site and pack on flight behavior could also be driven by management of sites, but all sites are managed by the same Broomfield Open Space and Trails department. Lastly, this relationship may reflect different patterns of human use at specific sites, which may drive coyotes to respond to human stimuli differentially.

Coyote habitat played a significant role in mediating urban coyote flight behavior. In recreational zones, coyotes were less likely to behave boldly and initiated flight behavior more quickly when presented with research observation as a stimulus. This response is

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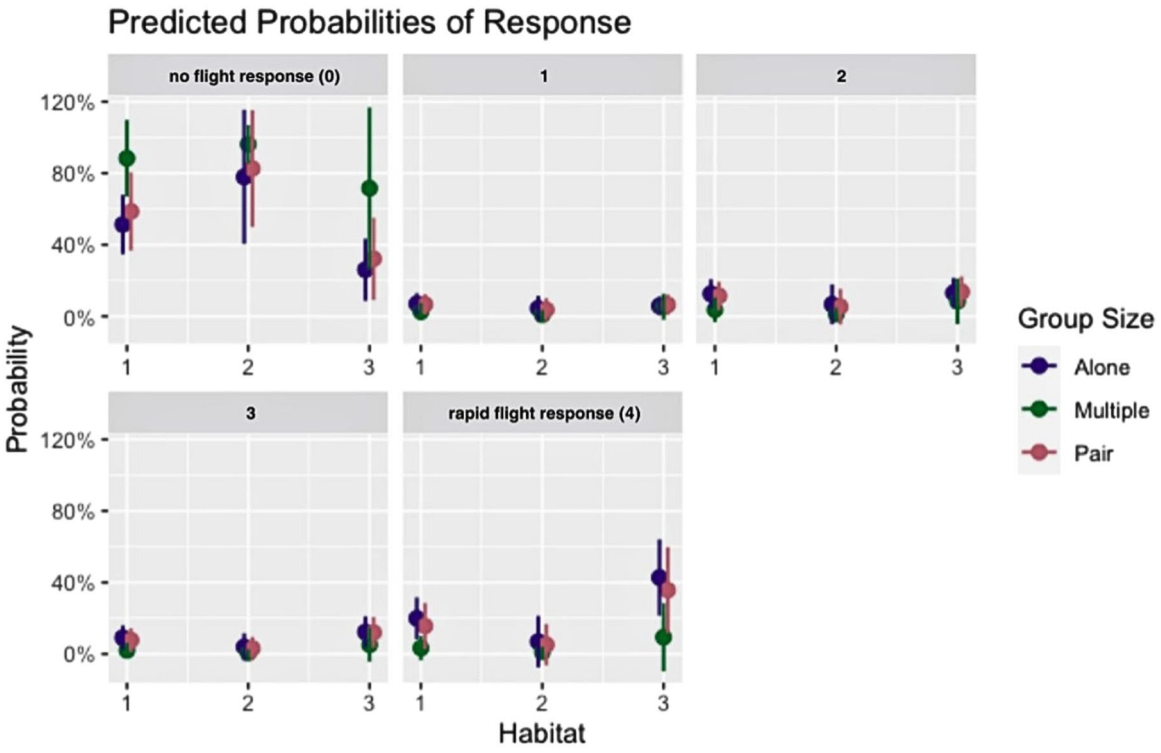


FIGURE 2 Coyotes have an increased probability of rapid, intense flight behavior in habitat 3, or recreational areas, especially when animals are alone or only in pairs.

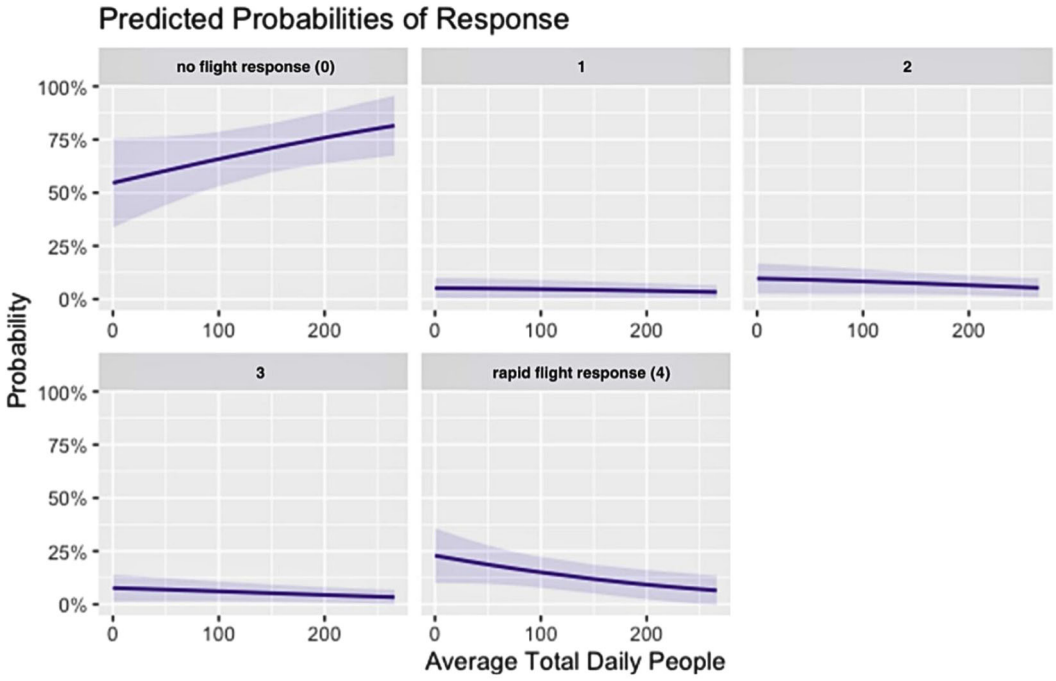


FIGURE 3 As average total daily visits go up, so does the predicted probability of a coyote not initiating flight (a score of 0). Additionally, as average total daily visits increases, the predicted probability of a rapid, intense flight response by coyotes (a score of 4) decreases.

representative of a reduced tolerance to the researcher, and people in general (Herrero et al., 2005; Samia et al., 2015). A more rapid flight response is the opposite of what we would expect if individuals were habituating to people. In fact, it is possible that coyotes in these microhabitats are experiencing a sensitization process—an excitatory neurophysical response in which neurons continue to discharge even after the stimulus has stopped (Groves & Thompson, 1970; Thompson & Spencer, 1966). Increased behavioral responsiveness and reduced tolerance over time is ultimately a mechanism by which animals can differentially react to stimuli that have historically had significant negative consequences (Richardson et al., 2013). Thus, the risk and perceived cost of enduring those pre-established, remembered consequences is greater than the cost of ignoring

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the stimulus. As with habituation, sensitization is a learned tradeoff that allows an individual to balance costs and benefits and optimize energetic expenditure and has been documented in diverse invertebrate and vertebrate taxa (Anton et al., 2011; Götz & Janik, 2011; Vollrath & Douglas-Hamilton, 2002).

Several reasons may explain why coyotes may be sensitized to humans in recreational landscapes. First, it is possible that the strength of stimulus in recreational landscapes (in this case, human and dog visitation) is either too intense or too inconsistent, or both (Groves & Thompson, 1970; Poon & Young, 2006). Additionally, it is possible that human behavior in these settings may be shaping response (Mackintosh, 1987; Rankin et al., 2009). Broomfield Open Space has devoted many resources to educating residents on appropriate coyote hazing techniques (Broomfield Open Space and Trails Department, n.d.), so it is possible that coyotes are being more intensely hazed in heavily frequented areas (though we neither observed nor measured this). Lowered tolerance in recreational zones could also be shaped by distance of the coyotes' core territory or den site from the recreational zone—circumstances in which they are more likely to behave more reactively to offset increased risk of being caught (Frid & Dill, 2002; Ydenberg & Dill, 1986). Coyotes' increased flight behavior in recreational areas may occur because of the ecological communities these microhabitats do, or more importantly, do not, support. Animals become sensitized and more reactive over time in resource-poor habitats where the risk of negative repercussions is not outweighed by the reward of procuring (high-value) food (Ydenberg & Dill, 1986). Thus, if recreational zones do not support enough potential food items coyotes are unlikely to remain in those landscapes when confronted with human disturbance stimuli. Large sports fields and paths are categorically low in vegetation cover and typically comprise only a few grass species. Forrest and Clair (2006) found that manicured areas of mowed grass had a lower bird and small mammal abundance, which matches what Mahan and O'Connell (2005) found in their study of mowed urban parks. Ćirović et al. (2015) also suggest that this is seen in European brown bears (*Ursus arctos*), as they suggest food availability was the reason bears were more frequently seen in forested habitats and avoiding agriculture and grasslands. This reduced prey density may make fleeing from stimulus in these areas more advantageous energetically than staying and risking enduring negative consequences from human disturbance.

Though our model suggests that coyote group size could potentially shape coyote flight behavior, we open with a caveat. We did not utilize any methods that would have supported our coyote group composition findings in the field—we had no collars or tracking devices to ensure the number of individuals we recorded was the true number of individuals. Due to the amount of vegetative cover in the sites, it is possible that there were coyotes present that we were unable to account for. Thus, it is possible that our group numbers were under reported. However, based on the data we were able to collect, we found a nearly significant, inverse relationship between coyote group size and flight behavior scores. When coyotes were in groups of more than two individuals, they were more likely to behave boldly. This follows established theories of how wildlife responds to another type of stimulus, predation pressure. Hamilton (1971) and Pulliam (1973) wrote about the benefits of increased group size when it comes to predation pressure, which would suggest that animals in larger groups may be more tolerant to predators and potentially other stimuli as well (Samia et al., 2015). It is also possible that grouped coyotes may have the opportunity to learn from each other how to behave in the face of nonaversive stimuli, which would contribute to the impact of pack grouping and site on urban flight behavior. However, in a systematic review of studies done on birds, Samia et al. (2015) found group size to be "less important in explaining variation in tolerance of human disturbance." We suggest that more work on the relationship between urban coyote group size and tolerance to people must be done by studies that would have a more complete understanding of coyote group composition so that we may better understand how group size may influence flight behavior, and thus tolerance and habituation, in shared spaces.

Notably, models including dogs as an independent variable did not perform well compared to models without them. This may be due to a lack of data on dog proximity to coyotes, dens, and coyotes' preferred habitat, or these findings could be reflective of open space management practices that prioritize keeping dogs on-leash and on-path. Over the course of our study season, we seldom observed off-leash dogs ($n = 2$), which kept most dogs from interacting directly with coyotes (there was only one instance of one off-leash dog directly interacting with a coyote, in which it was being chased by a coyote). For coyotes, then, because they may seldom interact with dogs, the presence of dogs may not be a highly aversive stimuli that elicits flight behavior.

Our findings lead to several recommendations for managers of wildlife in urban open spaces. First, because many instances of human–coyote conflict occur when coyotes are behaving boldly (Timm et al., 2004), a goal of management would be to prevent or reduce bold behavior in areas that are highly frequented by people and pets. Due to coyotes' reduced boldness in recreational areas, all of which are mowed and maintained by humans, it would be beneficial to have mowed buffer zones around paths and natural areas that are set aside for human or pet use. Second, because we have seen that as human recreational use increases, so too does coyotes' tolerance for human presence, we suggest that in shared urban landscapes, managers offer increased information or educational outreach about hazing practices (Broomfield Open Space and Trails Department, n.d.), which can be effective at separating people and coyotes (Bonnell & Breck, 2017). By doing so, managers may account for interactions amongst habituated coyotes and people, and reduce the chances of conflict occurring.

An additional goal of our work was to address the feasibility of using noninvasive, direct observational methods to study predator species in urban settings. We found that while it was possible to track and locate our study subjects, our ability to identify individual animals was likely lower than if working with radio-collared animals. Moreover, though we could differentiate among a few

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individuals, our study period was too short to learn all animals in the study area. For noninvasive research requiring knowledge of known individuals, more time must be allocated for individual identification as well as additional methods such as an extensive camera trap array. However, there are many reasons one may elect to conduct more wildlife behavior work noninvasively: there is a minimal budget, there is a reduced health and safety risk to the animals being studied, and it pushes researchers to rely on local, first-hand knowledge of animal presence and behavior. However, there are also several strengths to our study that we wish to highlight. We were able to conduct our work on a very limited budget, and we were also able to utilize time in the field and local knowledge of coyotes to directly observe coyote behavior. Thus, this type of noninvasive work may be useful to others who wish to study urban wildlife behavior with minimal funding.

We close by offering several caveats. First, our sample size of observations was small ($n < 100$ observations) which can lead to models with low explanatory power and inconclusive model evaluation, all of which can obfuscate important relationships and introduce unnecessary ambiguity (Bissonette, 1999). Second, our noninvasive methods were not successful at identifying individual-level responses, which Blumstein (2016) has called for to strengthen wildlife habituation research. Additionally, because we were tracking and locating coyotes in situ without any tracking technology, it would be difficult to definitively say when coyotes began responding to observers, as this may have occurred before researchers spotted the coyote. Future noninvasive work should focus on increasing the sample size of observations, either by increasing the length of the field season or by increasing the number of study sites. An increased field season may also allow researchers to solidify their ability to identify and track individuals without the use of telemetry.

AUTHOR CONTRIBUTIONS

Emily R. Golden Beam: Conceptualization (equal); data curation (lead); formal analysis (lead); funding acquisition (lead); investigation (lead); methodology (equal); project administration (lead); resources (supporting); supervision (equal); visualization (lead); writing—original draft (lead); writing—review and editing (equal). **Joel Berger**: Conceptualization (supporting); writing—review and editing (equal). **Stewart W. Breck**: Conceptualization (equal); methodology (lead); writing—review and editing (equal). **Christopher J. Schell**: Formal analysis (supporting); software (supporting); writing—review and editing (supporting). **Joanna E. Lambert**: Conceptualization (equal); methodology (equal); resources (lead); supervision (lead); writing—review and editing (lead).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and code will be available by email request to the corresponding author.

ORCID

Emily R. Golden Beam http://orcid.org/0000-0002-6358-0212
Joel Berger http://orcid.org/0000-0003-1498-9350
Christopher J. Schell http://orcid.org/0000-0002-2073-9852

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AUTHOR BIOGRAPHY



Emily R. Golden Beam is a PhD candidate working with Dr. Joanna Lambert in the Environmental Studies Department at University of Colorado Boulder. She focuses on how to study predator behavior in the Anthropocene both non-invasively and in ways that honor all stakeholders. Her work primarily takes place in the American West.

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