

Human densities, not pollution, affect urban coyote boldness and exploration

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Abstract

Comparative studies show that urban coyotes behave differently from their rural counterparts. However, these studies often treat cities as homogeneous. Cities feature diverse pressures for wildlife, such as variable human densities and environmental hazards, two factors that are known to drive increased risk-taking. Thus, this heterogeneity creates a shifting landscape of risk, which may drive locally adapted behavioral strategies within cities. Yet, the influence of these urban pressures on coyote behavior is not well understood. To investigate this, we conducted novel object testing at 24 sites across gradients of human density and pollution. We recorded coyote detections and coyote behavioral responses to the novel object, focusing on time spent alert, time spent close, and total exploration. We found that coyote detections varied with both human density and pollution, with coyote detections being markedly lower in areas with high human density and high pollution. Coyote boldness (time spent alert and close) and exploration were uniformly associated with human density, with coyotes in human-dense displaying elevated boldness and heightened exploration. Our results suggest that urban heterogeneity in human density impacts apex predator behavior, potentially having downstream consequences on human-carnivore coexistence.

1. Introduction

Cities are complex, coupled human-nature systems that establish variable landscapes of risk that pressure wildlife to rapidly adjust or face local extirpation¹⁻³. Because urban ecosystems challenge organisms with novel scenarios and disturbances that encourage phenotypic differentiation, research to date has focused on understanding how urban and rural populations differ. In particular, understanding how urban and rural individuals contrast in behavior, including boldness, an individual's response to a risky situation or event, and exploration, an individual's willingness to explore a novel situation, has been of large interest. This is because behavior is a particularly flexible trait that organisms alter in response to environmental cues^{4,5}. Indeed, urban individuals have been shown to diverge from their rural counterparts in several behaviors, including boldness, exploration, and aggression^{3,6}. Yet, this research approach has often treated cities as homogeneous, despite the strong landscape heterogeneity within and across cities^{7,8}. Within-city variation in disturbances, including humans and pollutants, may therefore also drive phenotypic divergence at a fine scale, perhaps even across neighborhoods⁹.

Human presence is typically cited as one of the most prominent factors driving alterations in wildlife ecology, including behavior¹⁰. For instance, urban wildlife are less likely to flee from humans compared to their rural counterparts¹¹⁻¹³, and this heightened tolerance is often used as a metric of boldness^{14,15}. However, human presence can be further delineated into two distinct features of urban environments that vary across neighborhoods: the "human footprint" (i.e., components of the built environment such as building density) and "human activity" (i.e., population size and foot traffic)¹⁶. Human footprint and activity can have differential effects on wildlife behavior, with larger carnivores, such as mountain lions (*Puma concolor*) and bobcats (*Lynx rufus*), reducing activity in, or avoiding, areas with high human

presence^{16,17}. Indeed, humans can mediate trophic interactions and shape predator assemblages across the urban matrix, allowing prey and smaller predators to avoid predation by selecting habitats with higher human densities or development^{16,18,19}; this phenomenon is called the human shield hypothesis²⁰. However, organisms in areas of high human activity face trade-offs: their access to natural habitat is relatively limited, with increased exposures to disturbances like noise pollution and environmental contaminants. Relaxed predation pressures and reduced natural habitat may therefore combine to bolster boldness and exploration in human-dominated environments^{21,22}, leading to the exploitation of anthropogenic resources for food and shelter. Variation in human footprint and activity within cities, as well as species-specific differences toward those disturbances, should induce behavioral variance across neighborhoods and species in a single city⁹.

In addition to the amount of natural habitat, the overall quality of habitat can also influence animal behavior. In cities, environmental quality is typically measured by the concentration of pollutants and contaminants (e.g., PM_{2.5}, pesticides, heavy metals)²³, which can have downstream consequences on wildlife behavior^{24,25}. Environmental pollutants and contaminants are particularly pervasive in cities, with detrimental consequences for organismal health and fitness²⁵. For instance, research has linked exposures to air toxins and metals such as chromium to DNA damage, elevated mutation rates, and heightened cortisol levels^{26–28}. Moreover, most human-produced pollutants are endocrine disruptors, altering the hormonal systems that are known to underpin behavioral traits like boldness, exploration, and activity^{29–32}. Rats exposed to high levels of diesel exhaust had poorer spatial memory and were less likely to recognize novel objects^{33–35}. Birds exposed to metal pollution were slower explorers, had altered migratory behavior, and reduced song repertoires^{36–39}. Fish exposed to environmental contaminants were generally bolder and exhibited slower or decreased exploration tendencies⁴⁰. Thus, contaminants can alter the behavioral traits of an individual that are critical in establishing and succeeding within cities, including boldness and exploration^{25,29,41,42}. Changes in behavior may scale up to affect community-level processes²⁵, with emerging work demonstrating that areas with greater environmental contamination have lower mammalian biodiversity and impacts mesocarnivore activity⁴³. However, the effect of contamination on wildlife ecology may vary by the city⁴³, and contamination can also have asymmetrical effects on species as a consequence of sensitivity to certain pollutants or differences in exposure²⁵.

Urban mesocarnivores, such as coyotes (*Canis latrans*), are an ideal model for investigating urban-induced behavioral changes⁴⁴. Urban coyotes, an apex predator in cities and flagship species for human-carnivore conflict, are bolder and more exploratory than non-urban coyotes^{45,46}. The behavioral adjustments observed in urban coyotes (e.g., diet flexibility⁴⁷, movement strategies⁴⁸) have greatly facilitated their adaptation to urban contexts across biomes and human disturbance regimes⁴⁴; yet those same shifts have exacerbated human-carnivore conflict^{49–51}. Though myriad studies have examined how coyotes are adapting to cities behaviorally along axes of urbanization, the effect of

contamination on coyote behavior remains uninvestigated (but see Hentati et al.⁴³). This is particularly pressing as due to their role as an apex predator, coyotes are particularly vulnerable to the effects of biomagnification^{52,53} and disruptions to carnivore behavior via ingestion or exposure to contaminants can alter community dynamics and ecosystem function by disrupting the top-down pressures carnivores exert on other wildlife. Hence, disentangling how human disturbances shape carnivore behavior is critical to maintaining healthy, functioning ecosystems.

To address these gaps, we used novel object testing to elicit a behavioral response^{45,54,55} and explore how human density and pollution were associated with coyote risk-taking behaviors (i.e., boldness and exploration). We also explored how the number of coyote detections varied with our landscape variables. We hypothesized that coyote risk-taking would vary with human density and pollution. Specifically, we predicted that high human densities would be associated with elevated boldness and exploration as previous work has demonstrated carnivores in human-dense environments show increased trait values for both behaviors^{45,56–59}. We also predicted that areas with high pollution would be associated with elevated boldness and increased exploration in both coyotes based on work in fish^{40,60}. Lastly, we predicted that coyote detections would be lowest in human-dense and polluted areas⁴³.

2. Methods

2.1 Study Area

This research was conducted at 15 public parks and 9 private residences across the East Bay region of Northern California between December 2022 and February 2023. The study included sites within the cities of Antioch (2022 estimated population density: 3,906 people per square mile), Berkeley (12,401 ppl/mi²), Oakland (7,725 ppl/mi²), and Richmond (3,758 ppl/mi²)⁶¹ (Fig. 1). The East Bay features a Mediterranean climate, characterized by mild temperatures throughout the year and wet, cooler winters—the conditions during the study period (mid-winter average high of 55°F and low of 42°F)⁶². Motion-activated trail cameras (Bushnell, Overland Park, Kansas, USA) were used at each location and operated for an average of 66 days. Each camera recorded 30-second clips with a one-second interval between triggers. Cameras were deployed only at locations where landowner consent was secured, with all sites spaced at least 1 km apart to align with territorial ranges typical of urban mammals, as established in previous studies^{63–65}.

2.2 Geospatial Processing and Data Analysis

We created a buffer around each camera site at 500m for extracting our landscape variables of human population density⁶⁶ and pollution⁶⁷. Due to a minimum camera spacing of 1km, we placed a 500m buffer to avoid potential spatial pseudo-replication between sites (similar to Lombardi et al.⁶⁸, for example). For pollution, we followed the methods in Estien et al.⁶⁹ and downloaded environmental hazard variables from CalEnviroScreen⁶⁷ to create a pollution burden score for each site. We extracted

the mean for the following variables: pm 2.5, diesel pm 2.5, toxic air contaminants, cleanup sites (i.e., brownfield sites), groundwater threat, hazardous sites, solid waste sites, lead risk from housing, traffic, and ozone. We then created a percentile such that a score of 0 would represent no pollution burden and 100 would represent a high pollution burden⁶⁹. We also considered the percentage of impervious surfaces as well as median household income, but these variables were highly correlated with our variables (Figure S1); therefore, we excluded these variables. After extracting the mean for human population density and pollution per site buffer (Figure S2), we calculated the median in our dataset and subsequently categorized each site as 'low' or 'high' per variable. All geospatial analyses were conducted in ArcGIS Pro using the 'Zonal Statistics' tool to extract the mean for all hazards.

2.3 Novel Object Test and Behavioral Coding

We used a paired-site design where each site ($n = 24$) served as both a control and treatment, with the order of condition randomized across sites. At each site, the testing period lasted at least 8 weeks and followed the methods in Breck et al.⁴⁵. Briefly, we dug a shallow hole in the ground and then filled it with a tablespoon of bait (Sweet Meat Predator Bait, Russ Carman, New Milford, Pennsylvania). The hole was then covered with the removed substrate. We placed a fatty acid scent tab (Pocatello Supply Depot, Idaho) on top of the covered hole as an additional attractant⁴⁵. Instances where only the bait and fatty acid tab were applied as described served as our control (Fig. 2A). For our treatment, we added a novel object consisting of four wood stakes in a 1m² square formation around the hole, with a single white rope threaded across the top of all stakes standing roughly 1m above the ground (Fig. 2B)⁴⁵. For the first four weeks, a site was randomly given the control (only bait) or the treatment (bait + novel object). For the last four weeks, if the site had first received the control, it then received the treatment, and vice versa. For each site, we coded several behaviors of interest (Table S1) and recorded the number of detections per species. For detections, videos within 30 minutes of each other were removed to ensure the independence of species triggers (i.e., temporal independence)^{43,70}.

To understand coyote responses to our novel object, we extracted data from each video (i.e., an observation) using Behavior Observation Research Interactive Software (BORIS)⁷¹. Any video that fell within 30 seconds of the previous video was considered the same observation with the same individuals. Within an observation, we recorded the time spent alert (i.e., being attentive to the surrounding environment) regardless of an individual's distance to the object. We recorded our remaining behaviors within one body length of the object (see Table S1 for Ethogram). When a species was within one body length of the object, we recorded the amount of time it spent close (i.e., being within one body length of the novel object). Time spent close also included time spent within the object's interior (i.e., between the wood stakes). We consider time spent close and time spent alert as our metrics of boldness. We then measured coyote exploration by recording the number of occurrences of the following behaviors: digging, sniffing, touching, and moving through the object. We then calculated the total number of times an exploratory behavior occurred per observation (i.e., total exploration). Thus, we identified bolder animals as ones that spent less time alert and more time close, and more exploratory animals as ones that have a higher total exploration metric.

Prior to coding, four observers were trained on the same 35 videos that we chose at random until > 80% interobserver reliability was achieved. We used Cohen’s kappa to assess interobserver reliability⁷², which was 85.67%. After coding was complete, behavioral data were cleaned to ensure the absence of behaviors (e.g., a coyote was not observed to be alert) was also captured (Supplemental Materials 1). In total, we recorded 313 behavioral observations for coyotes (Table 1), with 199 during the control and 114 while the novel object was present.

Table 1
Coyote detections in relation to human density and pollution.

Variable	Number of sites	Number of sites visited by coyotes	Total visits of coyotes	Total Behavioral Observations
Low human population density	12	8	226	255
High human population density	12	6	48	58
Low pollution	13	10	123	269
High pollution	11	4	150	44

2.4 Data Analysis

We conducted a preliminary analysis via linear mixed models and found that the testing condition order (i.e., control then object, or object then control) did not significantly affect the behaviors we coded for; however, observation number did, showing a strong negative effect on each coyote behavior. We also found that testing condition order did not impact the total number of detections observed at a site (Welch’s t-test $p = 0.884$), nor did we find a strong relationship between the number of days active and detections (Pearson’s correlation 0.119; Figure S3). Thus, we only included observation number as a fixed effect across all of our final models to control for the negative effect of time, which we expect was due to loss of potency, or complete removal, of the bait over time (e.g., dissipation, consumption, moving of bait by squirrel).

To test whether human density and pollution burden were associated with observed behaviors, we used zero-inflated negative binomial mixed models in the *glmmTMB* package to account for the high number of zeros in our dataset⁷³. We used a model selection approach to assess the suitability of various combinations of fixed effects, including testing condition, human density, pollution burden, and observation number. Our null model had observation number as the only fixed effect. Site was included as a random effect across all models. Model fit was assessed using Akaike’s information criterion (AIC) corrected for small sample size⁷⁴. Models within two $\Delta AICc$ were considered to be equally as likely as our best-performing model. From the top model, we extracted estimates (β), p-values, confidence intervals (CIs), and R-squared goodness of fit values (R^2). To compare the behavioral responses between variables in our models, we conducted Tukey’s pairwise comparisons using estimated marginal means from the best-performing model.

Lastly, we investigated how coyote detections varied across our landscape variables. To determine if human density and pollution burden had a significant effect on the total number of coyote detections at a site, we used a negative binomial model in the *glmmTMB* package⁷³. Human density and pollution were fixed effects, site was a random effect, and we included the number of days the camera was active per site as an offset variable, following similar methods to Hentati et al.⁴³.

3. Results

3.1 Detections

Across 24 sites, we received 274 coyote detections in total across 14 sites (Table 1). Human densities negatively affected coyote detections ($\beta = -1.625$, CI: -3.056, -0.194, $p < 0.05$; Figure S4; Table S2), with 48 detections in high human density areas compared to 226 detections in low human density areas. Similarly, pollution negatively affected coyote detections ($\beta = -3.031$, CI: -4.991, -1.071, $p < 0.01$; Figure S4; Table S2), with 238 and 36 detections in sites with high and low pollution burden, respectively.

3.2 Boldness and Exploration

Our top model for time spent alert was our human density and treatment model and held most of the support (weight = 0.79). Models with the greatest support for time spent alert indicated that human density and treatment interacted to affect the amount of time coyotes spend alert (Table 2; S3). Generally, coyotes decreased their time spent alert in areas with high human density, and while the novel object was deployed (Table 2). When considering the interaction between human density and treatment, we had three findings. First, during the control period (i.e., attractant only), we found that coyotes spent significantly more time alert at sites with low human density ($\beta = 1.497$, $p < 0.01$; Fig. 3A). Second, we found that during the object period (i.e., novel object and attractant, we found no significant differences between time spent alert between sites with low and high human density (Fig. 3A). Lastly, when we compared behavioral responses to each treatment per human density category, we found that coyotes at sites with low human density were significantly less alert during the object period relative to the control ($\beta = 0.791$, $p < 0.01$), whereas coyotes at high human density sites showed no significant differences (Fig. 3A).

Table 2

Parameter estimates for best-performing coyote risk-taking with human disturbances models.
Significant terms are bolded.

Behavior	Model	R^2_c	Term	Estimate	SE	Pr (> z)	95% CI
Time Spent Alert	Human Population Density * Treatment	0.370	Intercept	3.468	0.146	< 0.001	3.182, 3.753
			Human Density (High)	-1.497	0.404	< 0.001	-2.288, -0.705
			Treatment (Object)	-0.792	0.213	< 0.001	-1.209, -0.375
			Observation Number	-0.043	0.009	< 0.001	-0.061, -0.247
			Human Density (High) * Treatment (Object)	0.976	0.496	< 0.05	0.004, 0.497
Time Spent Close	Global	0.531	Intercept	3.822	0.153	< 0.001	3.522, 4.123
			Pollution Burden (High)	0.460	0.270	0.089	-0.070, 0.990
			Treatment (Object)	-1.990	0.253	< 0.001	-2.486, -1.494
			Human Density (High)	-1.452	0.313	< 0.001	-2.065, -0.839
			Observation Number	-0.065	0.008	< 0.001	-0.082, -0.049
			Pollution (High) * Treatment (Object)	-1.260	0.665	0.058	-2.564, 0.044
Exploration	Global	0.456	Intercept	0.997	0.222	< 0.001	0.561, 1.433
			Human Density (High)	-1.008	0.435	< 0.05	-1.861, -0.154
			Treatment (Object)	-2.306	0.350	< 0.001	-2.993, -1.620

Behavior	Model	R^2_c	Term	Estimate	SE	Pr ($> z $)	95% CI
			Observation Number	-0.043	0.011	< 0.001	-0.065, -0.022
			Human Density (High) * Treatment (Object)	1.337	0.628	< 0.05	0.106, 2.568

The top two models for time spent close were our global model (weight = 0.54) and our human density-treatment interaction model (weight = 0.46), providing strong support for the effect of human density and treatment on this behavior (Table 2). We found identical trends for time spent close observed in time spent alert, with coyotes generally spending less time close while the novel object was present and in areas with high human density (Table 2). During the control period, we found that coyotes spent significantly more time close at sites with low human density ($\beta = 1.452$, $p < 0.001$; Fig. 3B). In contrast, during the object period, we found no significant differences between time spent close between sites with low and high human density (Fig. 3B). When we compared behavioral responses to each treatment per human density category, we found that coyotes at sites with low human density were significantly less close during the object period relative to the control ($\beta = 2.620$, $p < 0.001$), whereas coyotes at high human density sites showed no significant differences (Fig. 3B).

Lastly, for total exploration, our top models were the human density-treatment model (weight = 0.60) and treatment model (weight = 0.26), indicating that both human density and treatment strongly affect coyote exploration. We found similar trends in exploration across human density as seen in time spent alert and close, with coyotes exploring less while the novel object was deployed and at sites with high human density (Table 2). When we compared exploration during the control period, we did not find any differences in coyote exploration (Fig. 3C). Similarly, we did not find any differences in coyote exploration when we compared the object period. Finally, when we compared the control and novel object period, we found that coyotes at sites with low human density explored significantly less during the object period relative to the control ($\beta = 2.306$, $p < 0.001$), whereas coyotes at high human density sites showed no significant differences (Fig. 3B).

4. Discussion

Here, we provided evidence suggesting that within-city variation in human densities and pollution affect coyote ecology. First, we found that the number of coyote detections varied with both human density and pollution, with fewer coyote detections being observed in areas with high human density and high pollution. We also found that pollution had a stronger negative effect on coyote detections than human density, suggesting that habitat quality may be a better predictor of coyote activity than human density. Second, we found that coyote boldness and exploration are uniformly associated with human density. These results suggest that factors associated with human density, such as risk and habituation, drive

coyote risk-taking rather than pollution burden. Overall, our results suggest that human densities and pollution differently affect aspects of coyote behavioral ecology, offering insight into how coyotes are adapting to urban environments.

We found that coyote detections were markedly lower in areas with higher human densities and higher pollution, similar to emerging research by Hentati et al.⁴³. Although coyotes are highly adapted to cities, both social and ecological factors limit their population size, including human-coyote conflict that can lead to lethal removal and finite habitat and territory availability⁷⁵. First, despite the high potential reward of food or other resources (e.g., space, water), areas of high human densities create societal tension for coyotes. Though areas of high human density may have more green space for recreation and other human activities, coyotes that inhabit those greenspaces face a higher probability of conflict and removal^{51,75}. In contrast, high human density areas can have a high concentration of people and buildings, creating finite prey resources and priming situations for potential negative human-coyote interactions to occur – such as raiding trash cans, moving through yards for food, or extremes like attacking pets. In parallel, ecological resources can similarly limit coyotes in urban areas. Within our study area, ecological resources that coyotes rely on for successfully establishing a territory, such as green space availability, are not evenly distributed as a result of legacies of injustice⁷⁶. Redlining in particular, a policy that denied credit and financial services to individuals based on ethno-racial identity^{77,78}, has been linked to reduced environmental quality (e.g., less vegetation, high pollution), reduced biodiversity, and altered species assemblages in California^{69,79}. These areas also have barriers, such as the 580 and 880 highways, that may impede the dispersal and movement of coyotes from greenspaces and richer habitats into areas with higher pollution. Thus, as a consequence of injustice, coyotes in our study area are detected less in areas with more pollution due to the lack of available green space, reduced vegetation, and movement barriers.

Our work builds upon previous literature suggesting that urban coyotes are bolder than rural conspecifics^{45,56}, with boldness varying as a function of human presence^{46,58,59}. We found strong support for our human density hypothesis in coyotes. First, at high human density sites, coyote alertness and proximity did not differ between treatments, whereas at sites with low human density, coyotes spent less time close and alert while the novel object was present. Second, in the control condition, coyotes inhabiting low-density areas spent more time alert and close to the attractant, suggesting heightened wariness of human presence. Coyotes are customarily wary of novel stimuli in both field and captive settings^{80–82}. However, individuals with greater experiences of people in both the wild⁵⁶ and captivity⁸³ display greater tolerance of human presence and infrastructure. In addition, increased consumption of human food subsidies in cities is thought to promote coyote boldness via associative learning^{84,85}, which may reduce fear of humans and associated disturbances (e.g., objects, sounds)^{56,83,86,87}. Additionally, the absence of apex predators (e.g., mountain lions and wolves) that might otherwise temper risky behaviors could also encourage coyote boldness in cities^{21,88}. Consistent coyote responses across our treatment conditions in human-dense areas provide additional evidence to support the claim that increased human densities are potentially driving coyote tolerance to human-induced novelty.

We also found that coyote exploration, as measured by total exploratory behaviors, is driven by human density. Urban coyotes are known to be more exploratory than their rural counterparts⁸⁵, and if urban coyotes have an extensive history of exploring novel features due to a higher frequency of encountering novelty, coyotes at sites with high human densities may be demonstrating habituation to novelty. For instance, coyotes in areas with high human densities may be exposed more frequently to stimuli such as trash cans, fences, scents, and human infrastructure, compared to coyotes in areas of lower human density. Our additional finding that coyotes at sites with high human density do not significantly change the number of exploratory behaviors directed towards the novel object, unlike coyotes at sites with low human density which reduced their exploration, further supports this hypothesis. However, further research is needed to explicitly investigate if coyotes increase or decrease their exploration when exposed to novel stimuli repeatedly (but see Garcia, Parsons, and Young⁸⁹ and Young, Touzot, and Brummer⁹⁰).

Surprisingly, we did not detect an effect of pollution on coyote risk-taking for the above behaviors. Though current work in birds^{38,39} and fish⁴⁰ demonstrate that individuals who face greater exposure to pollutants have altered risk-taking, the relationship between pollution and risk-taking is far from consistent^{91–93}. For example, although urban great tits were slower explorers at sites with more metal pollution, aggression and nest defense showed no relationship to metal pollution³⁸. Similarly, neophobia was unrelated to toxic metal exposure but was more related to urban disturbances⁹¹. We may not have detected an effect of pollution on coyote behavior due to the coarseness of our environmental hazard variables at the census tract level. Coyotes may be exposed to, for example, air pollutants such as pm 2.5 in their local habitat which is known to vary at very fine spatial scales^{94,95}. Hence, to disentangle the effect of environmental contamination on coyote behavior within cities, a better approach may be to sample locally via air quality monitors and soil samples to understand site-level exposure to pollutants. Similarly, other relevant contaminants, such as rodenticides, pesticides, and heavy metals, were not included in our pollution metric and may have adverse impacts on coyote behavior²⁵.

Our results point to coyotes in high human density areas exhibiting elevated boldness and heightened exploration. These findings point to several potential mechanisms to infer how the coyote behaviors we documented vary as a function of human density. First, habituation or learning may be driving elevated risk-taking in areas of high human density. In areas with more people, coyotes are exposed to a myriad of novel physical, visual, and olfactory stimuli. Through repeated exposure, coyote responses to risky stimuli (e.g., novel objects, loud noises) diminish leading to no marked differences between the absence of a novel object and the introduction of one as seen in our study. Second, these findings point to differences in the perception of overall risk between low and high human density areas. Areas of high human density have reduced predator assemblages, which can promote boldness and exploration^{21,22}. Hence, the absence of natural predators, namely mountain lions, primes coyotes to behave more with more risk by, for example, coyotes in human-dense areas not spending as much time alert during our control. Additionally, coyotes in high human density areas encounter risk more frequently than other conspecifics, including vehicles, people, and other disturbances associated with cities. Hence, because

coyotes must mitigate risk frequently, they are able to assess and determine the threat of novelty and adjust behaviors if necessary. In our study, this is reflected by human-dense coyotes not adjusting their behaviors in the face of novelty, unlike their non-human-dense counterparts who reduced their risk-taking when presented with novelty via reductions in exploration and time spent close. Lastly, development is also a salient factor that could be driving our behavioral observations. Captive research has shown that bold coyotes produce litters that are even bolder⁸³ and thus, coyote pups that are raised by bold parents likely have personality traits that yield riskier behaviors. Regardless of the mechanism, our results suggest that behavioral strategies in coyotes differ across urban landscapes as a function of people, rather than being monotonic.

In summary, we provided evidence to suggest marked differences in coyote behavioral traits within cities. We demonstrated that coyote detections across the landscape as a function of pollution and human densities, while coyote risk-taking varied with differences in human density. Further research is needed to disentangle the exact mechanisms that lead to changes in behavioral strategies, and if these strategies are consistent across other urban mesocarnivores. Our results provide critical insight into urban coyote behavioral ecology, creating a foundation to further explore how intra-city variation influences traits that predict individual success in urban areas, and what these behavioral changes mean for potential downstream consequences for human-carnivore interactions in cities.

Declarations

Author Contribution

COE and CJS designed the research project. COE and LAS conducted fieldwork. COE led the coding of videos. COE led statistical analyses, with support from LAS and CJS. COE wrote the first draft of the manuscript. COE made the figures. COE, LAS, and CJS edited the manuscript.

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Data Availability

The data analyzed for the study are available from the corresponding author on reasonable request.

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Figures

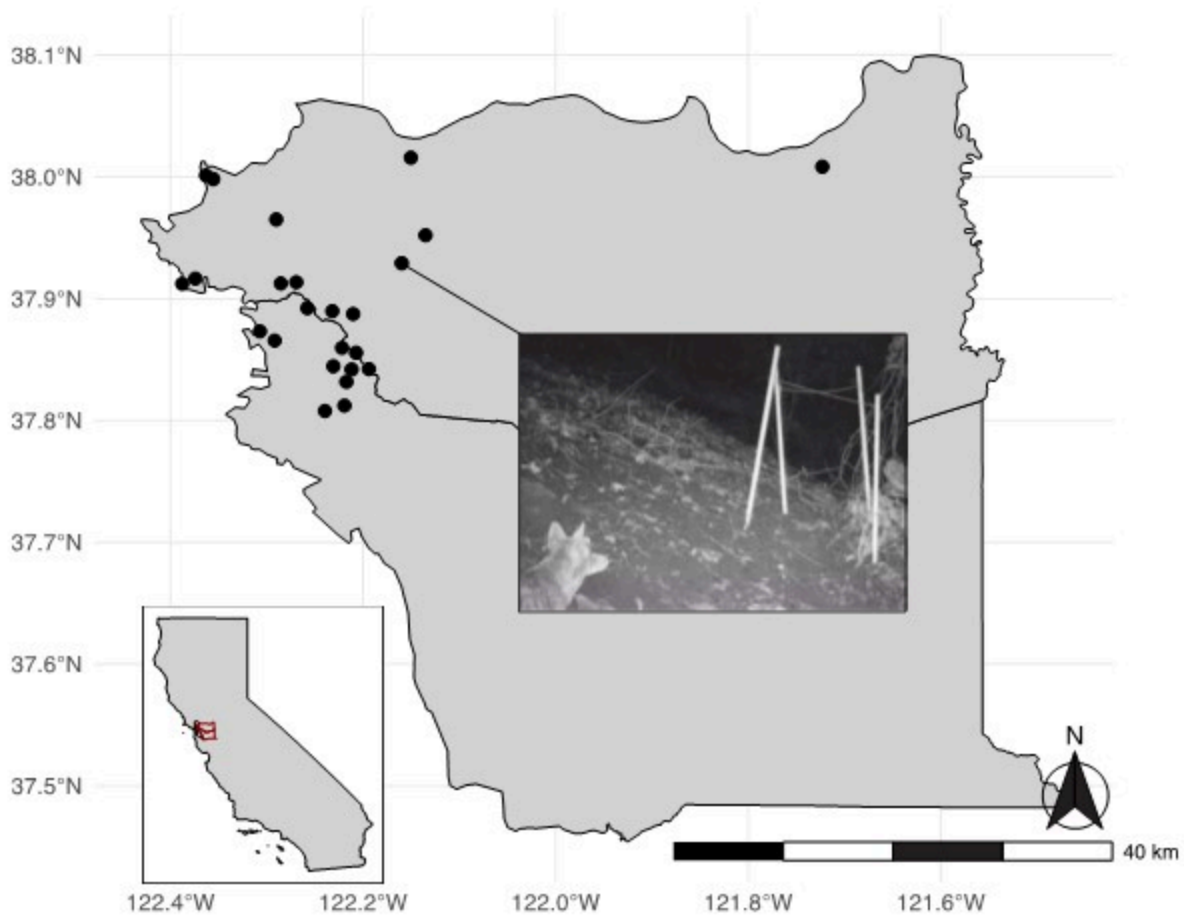


Figure 1

Study Area Overview. A map of the experimental sites located in the East Bay Region of the Bay Area in Northern California. Each dot represents a camera.

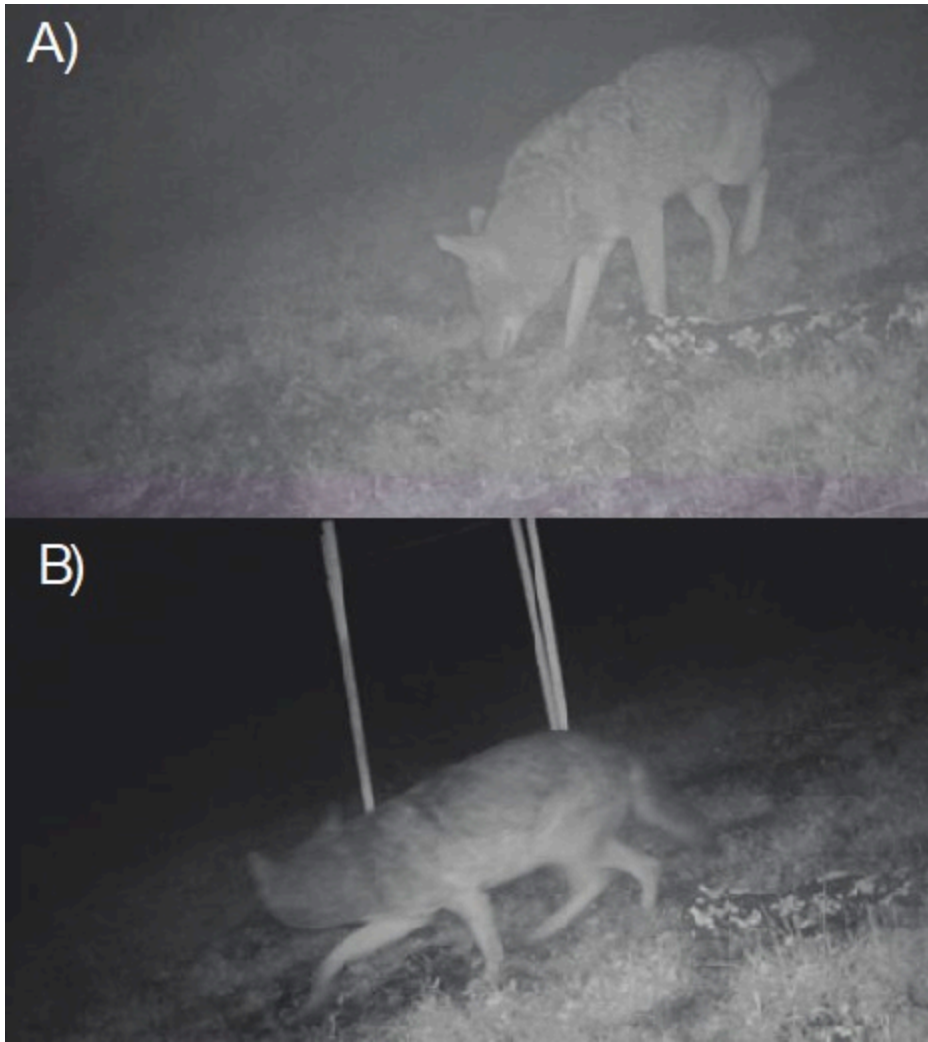


Figure 2

Images of coyotes interacting with our treatments. The top image (A) shows a coyote interacting during the control period (attractant only). The bottom image (B) shows a coyote interacting during the novel object period (attractant and novel object).

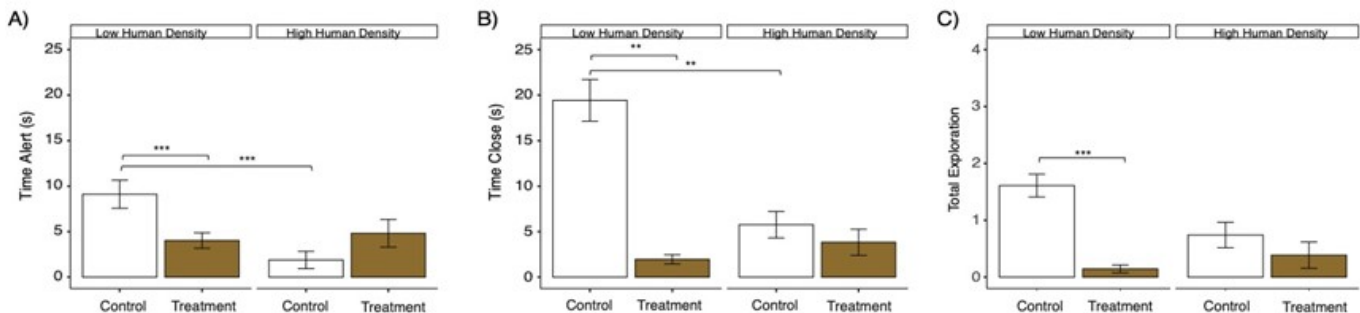


Figure 3

Coyote risk-taking in relation to human density and pollution. The top row shows (A) time spent alert, (B) time spent close, and (C) total exploration in relation to human density. The control (novel scent) is

shown in white, and the treatment (novel object and scent) is shown in brown. P-values are extracted from pair-wise Tukey comparisons of the estimated marginal means from the best-performing model for each behavior.

Supplementary Files

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