Using a novel framework of animal space-use behaviors reveals a gradient of responses to human modification

Nicole Gorman[1], Mike Eichholz[2], Daniel Skinner[3], Peter Schlichting[3], and Guillaume Bastille-Rousseau[4]

[1]Virginia Polytechnic Institute and State University
[2]Southern Illinois University
[3]Illinois Department of Natural Resources
[4]Southern Illinois University Carbondale

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Abstract

Spatial behavior, including home-ranging behaviors, habitat selection, and movement, can be extremely informative in estimating how animals respond to landscape heterogeneity. Responses in these spatial behaviors to factors such as human modification and resources on the landscape can highlight a species' spatial strategy to maximize fitness and minimize risk. These strategies can vary on spatial, temporal, and individual scales, and the combination of behaviors on these scales can lead to very different strategies among species. Harnessing the variation present at these scales, we developed a framework for predicting how species may respond to changes in their environments on a gradient ranging from generic, where a species exhibits broad-stroke spatial responses to their environment, to nuanced, in which a species uses a combination of temporal and spatial strategies paired with functional responses in selection behaviors. Using 46 GPS-tracked bobcats and coyotes inhabiting a landscape encompassing a range of human modification, we evaluated where each species falls along the generic-to-nuanced gradient. Bobcats and coyotes studied occupied opposite ends of this gradient, using different strategies in response to human modification in their home ranges, with bobcats broadly expanding their home range with increases in human modification and clearly selecting for or avoiding features on the landscape with temporal consistency. Meanwhile, coyotes did not expand their home ranges with human modification, but instead displayed temporal and spatial adjustments in their functional responses to human modification. These differences in response to habitat, resources, and risk between the two species highlighted the variation in spatial behaviors animals can use to exist in anthropogenic environments influenced by interspecific variation in behavioral plasticity. Categorizing animal spatial behavior based on the generic-to-nuanced gradient can help in predicting how a species will respond to future change based on their current spatial behavior.

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Keywords

Animal movement, spatial ecology, mesocarnivore, resource selection, human land modification, functional response

Introduction

Movement behavior is informative in capturing how animals respond to the heterogeneity in their environment. These responses include broad-scale decisions in the size and location of the home range (Burt 1943) as well as finer scale responses to heterogeneity in the environment through habitat selection decisions (Johnson 1980). Animals often vary in their movement behavior, which can be due in part to individual personality (Réale et al. 2010, Kaiser and Müller 2021), or plasticity in individual- or population-level behavior (Stamps and Groothuis 2010, Snell-Rood 2013). This variation can lead to directional reactions of animals to their environment, known as functional responses, which can include reactions to habitat (Mysterud and Ims 1998, Newediuk et al. 2022), prey (Holling 1965), forage (Spalinger and Hobbs 1992), or other stimuli. Functional responses of animal spatial behavior to anthropogenic factors have been documented in various species, including in wolf (*Canis lupus*) (Hebblewhite and Merrill 2008), caribou (*Rangifer tarandus caribou*) (Moreau et al. 2012), and moose (*Alces alces*) (Beyer et al. 2013) habitat selection and proximity to humans. Habitat selection is a particularly informative behavior to study because of the direct link between the spatial choices an individual makes and variability in the environment (Johnson et al. 2002), and because it can have direct implications for an animal's fitness (Nilsen et al. 2004, Mayor et al. 2009). Habitat selection and functional responses are especially important in the context of anthropogenic change, when landscape compositions are constantly undergoing modifications.

Animals can display a wide range of responses toward anthropogenic factors. These responses can range from generic, or broad-scale (hereafter referred to as generic responses), such as consistently avoiding human activity or structures in their home range (Muhly et al. 2011, Leblond et al. 2013), and which could lead to increased home range size for individuals inhabiting areas with greater levels of human modification (O'Donnell and delBarco-Trillo 2020). At the other end of this gradient, species can display nuanced, or refined, responses (hereafter termed nuanced responses) to humans, such as only avoiding anthropogenic features at a fine scale and during a certain periods of the day (Tigas et al. 2002), seasonally (Johnson et al. 2005), or by using a combination of spatiotemporal responses (Knopff et al. 2014). Investigating individual and temporal variation in spatial behavior can elucidate broader patterns in behavior, linking spatial ecology and animal behavior (Hertel et al. 2020), as well as help draw conclusions about population-level relationships with habitat (Bastille-Rousseau and Wittemyer 2019). Here, we propose that a multi-faceted characterization of a population that includes individual, spatial, and temporal variation in space use form the basis of characterizing where a population or species fall along a "generic-to-nuanced" gradient in spatial responses. This gradient is especially informative in characterizing animal responses to anthropogenic activities, which can also be particularly useful for wide-ranging species which use a variety of habitats with varying levels of human development.

Bobcats (*Lynx rufus*) and coyotes (*Canis latrans*) are two mesocarnivores that fill the role of top predator in the absence of large predators throughout much of North America (Laliberte and Ripple 2004, Roemer et al. 2009, Lesmeister et al. 2015). Bobcats are strictly carnivorous and are believed to prefer forested habitat above other habitat types (Litvaitis and Harrison 1989, Lesmeister et al. 2015). Coyotes are more generalist in both diet and habitat and are found in all habitats along a forested-to-rural gradient (Randa and Yunger 2006, Lesmeister et al. 2015), and are more likely than bobcats to exploit agricultural landscapes (Litvaitis and Harrison 1989, Nielsen et al. 2017). Both bobcats and coyotes have been observed to expand their home range with increased fragmentation, but coyotes are more plastic and adaptable to anthropogenic change, exploiting small resource patches on a landscape scale, regardless of connection (Riley et al. 2003, Atwood et al. 2004). Although mesocarnivores are a group expected to adapt better than other species to human development (Červinka et al. 2014, Streicher et al. 2021), they experience a spectrum of adaptability to coexistence with humans based on flexibility in diet and suitable habitat, as well as plasticity in behaviors like boldness and neophilia, leading to a variety of responses to anthropogenic land modification (Réale et al. 2007, Mason et al. 2013).

Here we studied how variation in anthropogenic activity shapes movement behaviors of these mesocarnivore species and characterized where they belong on the "generic-to-nuanced" gradient. Specifically, we investigated how a gradient of human modification impacted home range size and habitat selection of both species. We also evaluated how habitat selection behaviors vary temporally and how individual variation in this behavior could be linked to variation to the intensity of human modification for an individual (functional response). Overall, given the behavior of both mesocarnivores, we expected bobcat responses to be on the generic end of the gradient, marked by stronger and more consistent avoidance of human activities and overall larger home range when exposed to human activities. Meanwhile, we expected coyote responses to be more nuanced, with home-ranging behaviors less affected by human modification, but with space-use showing more individual variation, temporally-acute selection behaviors, and complexity in their functional responses to human modification.

Methods

Study Area

Our study occurred at two sites in Illinois. The southern Illinois study site is made up of Touch of Nature Environmental Center (37.62762, -89.15827) and Giant City State Park (37.60195, -89.18925), making up a combined 28.6 km^2 of Southern Illinois University- and state-managed land dominated by contiguous oak-hickory forest, with an average annual temperature of 14.1°C and an average annual precipitation of 118 cm (NOAA 2021). The central Illinois study site consists of state- and U.S. Army Corps of Engineers-managed properties surrounding Lake Shelbyville (39.51856, -88.70658). The landscape consists of a patchwork of private properties, public land, and small towns. The land is dominated by row crop corn and soybean agriculture, with some lakeshore and remnant forested patches. This study site has an average annual temperature of 12.2°C and average annual precipitation of 120 cm (NOAA 2021).

Capture and Handling

Bobcats and coyotes in both study sites were captured using cage traps (Tomahawk Live Trap, Hazelhurst, Wisconsin, Model 209.5, and homemade traps with similar dimensions, Beltrán and Tewes 1995) and rubber-padded foothold traps (Minnesota Trapline Products, Pennock, Minnesota, MB-650-RJ, Skinner and Todd 1990) during four winter capture seasons from January through March 2018 and 2019 and mid-November through March 2019-2020 and 2020-2021. Bobcats were chemically immobilized with ketamine and xylazine and recovered inside a cage trap before release (ZooPharm, Beltrán and Tewes 1995). Coyotes were chemically immobilized with BAM^{TM} (butorphanol tartrate, azaperone, and medetomidine hydrochloride) and were reversed post-handling with naltrexone and atipamezole before release (ZooPharm, Butler et al. 2017). All captured animals were fitted with LiteTrack Iridium 250 GPS collars (Lotek Wireless, Newmarket, Ontario, Canada) equipped with a release mechanism to drop off. Most collars recorded GPS locations once every 1.5 hours but 14 collars had a different schedule (1, 2, 3, or 4 hours).

Spatial Covariates

Several spatial covariates were used to delineate seasons and analyze resource selection. Landcover covariates were sourced from a 30 m resolution National Land Cover Database classification (USGS 2021) and reclassified into six landcover categories (water, exurban, grassland and scrub, forest, agriculture, and wetland) for seasonal delineation and four landcover categories (exurban, forest, agriculture, and other) for resource selection analyses. We also included a human modification covariate using a global layer which accounts for 13 anthropogenic global stressors at a 1 km resolution (Kennedy et al. 2019). We reprocessed a layer of Illinois streams and shorelines to create a Euclidean distance to water covariate at a 30 m resolution (Illinois State Geological Survey Prairie Research Institute 2015) and took the natural logarithm of the Euclidean distances to account for decreasing impact of a water source with increasing distance (Lehman et al. 2016). Similarly, we reprocessed a layer of Illinois paved roads to create a natural logarithm of the Euclidean distance to road covariate at a 30 m resolution (Illinois Technology Transfer Center 2020).

Home Range Size

To estimate the annual home ranges of bobcats and coyotes, we used autocorrelated kernel density estimation (AKDE), as developed by Fleming et al. (2015). We used the package 'ctmm' in Program R (Calabrese et al. 2016) to estimate home ranges. Home range sizes were calculated using the Ornstein-Uhlenbeck with foraging (OUF) model using a 0.95 quantile. In cases where AKDE estimation was not possible due to variogram abnormalities, annual home ranges were generated using KDE (Worton 1989).

We used two-sample t-tests to identify within-species differences in home range size, comparing differences in sex and study site (Laundré and Keller 1984). We also used univariate regressions to evaluate how the proportion of human modification in each home range (Kennedy et al. 2019) impacted home range size in both species. Intercept-only, linear, and quadratic regressions were performed and compared using the Akaike Information Criterion with correction for small sample size (AIC_C) to determine the top regression model (Burnham and Anderson 2002). We excluded transient individuals from the home range analysis because they made long-distance movements and did not establish home ranges during the tracking period.

Temporal Period Delineation

We used a clustering algorithm to define seasons ecologically (Basille et al. 2013). To define bobcat and coyote seasons, the movement speed and turning angle between successive locations were calculated for each individual. Using a moving window of time, we calculated the mean speed and tortuosity, as well as the proportion of the locations in water, exurban, grassland and scrub, forest, agriculture and wetland landcover areas within the moving window (USGS 2021). The DD-weighted gap method (Yan and Ye 2007) was used to determine the optimal number of clusters (seasons). We then used K-means clustering analysis (MacQueen 1967, Hartigan and Wong 1979) to identify clusters of similar space use behaviors to define seasons, adjusting bootstrap thresholds and windows of seasonal length to ensure continuous seasons of adequate length.

Day, night, and crepuscular diel periods were also delineated (Supporting Information). Equinox dates (NOAA 2018) were used to divide the year into four periods, and the average sunrise and sunset time for each period was calculated (MapLogs 2018) to account for changes in day length between the four periods (Thornton et al. 2004). Day was delineated as two hours after sunrise to one hour before sunset, night as two hours after sunset to one hour before sunrise, and crepuscular as the two lengths of time one hour before to two hours after sunrise and sunset (Franckowiak et al. 2020).

Resource Selection Functions

To determine individual-level habitat selection, we used a logistic regression to estimate resource selection functions (RSFs) for each individual within the annual home ranges (Manly et al. 2002, Bastille-Rousseau and Wittemyer 2019). The transient individuals that were previously excluded from home range size analysis were included in the RSFs, using KDE annual home range estimations (instead of AKDE). Twelve thousand random locations were generated within each of these home ranges. Each random location was also assigned a random date and time (Bastille-Rousseau et al. 2015), and the previously described temporal periods were applied to each used and random point so that each point was categorized based on its season and diel period.

Bobcat and coyote RSFs were estimated using the package 'IndRSA' in Program R (Bastille-Rousseau and Wittemyer 2019). 'IndRSA' estimates an individual-level RSF for each individual and a population average in a second step (Murtaugh 2007). K-fold cross-validations were performed for each output, and those with a k-fold value less than 0.2 were excluded from the results. Landcover categories, human modification, distance to water, and distance to road covariates were extracted for each used and random point. Landcover categories included the dummy variables of forested (reference category), agricultural, exurban, and other. The continuous variables of human modification, distance to water, and distance to road covariates were scaled so they could be compared to ease interpretation (Schielzeth 2010). Models for each permutation of species and temporal period were estimated in this manner.

Impacts of Human Modification on Predator Behavior

We estimated how human modification directionally affects bobcat and coyote resource selection behavior in the form of functional responses in habitat selection (Hebblewhite and Merrill 2008, Moreau et al. 2012). We used univariate regressions with the individual RSF coefficients for five covariates (agriculture, exurban, and other landcover; distance to water; and distance to road) as the response variables and the proportion of human modification in each home range (Kennedy et al. 2019) as the explanatory variables. These regressions were separated based on temporal period to discern temporal effects on these functional responses. In addition, regressions of the means of coefficients for each covariate during all temporal periods for each level of human modification in home range (each individual) were performed to find if a broad functional response was present regardless of temporal period. Weighted regressions were used to account for uncertainty associated to the RSF coefficients (Bastille-Rousseau et al. 2021). Intercept-only, linear, and quadratic regressions were compared using AIC_C to determine the top regression model (Burnham and Anderson 2002). The "other" landcover category lacked biological meaning, so was not included in the final results (Supporting Information).

Results

Fifteen bobcat-years (female n =7, male n =8, central Illinois n =4, southern Illinois n =11) and 31 coyote-years (female n =12, male n =19, central Illinois n =23, southern Illinois n =8) of location data were collected from 13 individual bobcats and 31 individual coyotes over the four trapping seasons. An average of 1,397 GPS locations were obtained from each bobcat (range 293-2,695) and an average of 1,736 locations were obtained from each coyote (range 213-3,596). Fourteen bobcat-years and 28 coyote-years of GPS data were used to calculate four bobcat and four coyote ecological seasons (Supporting Information). Bobcats had short, distinct seasons in fall, early winter, and late winter, but had one long season during spring and summer. Coyotes had short seasons during early and late winter and two longer spring and summer/fall seasons. The four seasons and three diel periods (day, night, crepuscular) were combined with the ecological seasons to create twelve bobcat temporal periods and twelve coyote temporal periods.

Home Range Size

After excluding three bobcats and six coyotes that exhibited transient movement behavior, 35 annual home ranges were estimated using AKDE and two were estimated using KDE (Figure 1). Bobcat mean home range size was 32.0 km^2 (n =12, range 2.5-132.0 km^2) and coyote mean home range size was 213.3 km^2 (n =25, range 7.1-849.0 km^2) (Supporting Information). Bobcat home ranges were significantly smaller than those of coyotes (t=-2.297, DF=35, p=0.028). There was no difference in home range size between bobcat males and females (female n =6, male n =6, t=-1.487, DF=10, p=0.168), but home ranges in central Illinois were significantly larger than those in southern Illinois (central Illinois n =2, μ=115.1 km^2, southern Illinois n =10, μ=15.3 km^2, t=9.409, DF=10, $p<0.001$). There was also no difference between male and female coyote home range size (female n =10, male n =15, t=-0.318, DF=23, p=0.753) or between study sites (central Illinois n =19, southern Illinois$n$ =6, t=0.249, DF=23, p=0.806).

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Figure 1. Left panel: Population-level bobcat and coyote home range size estimations using AKDE and KDE. Right panels: Bobcat and coyote AKDE and KDE home range size estimations by sex and study site separated by species. Asterisk indicates significant difference in home range sizes (α=0.05).

The home range size of individual bobcats had a quadratic relationship with the proportion of human modification within their home ranges (Supporting Information), with increased human modification being correlated with larger home ranges (Figure 2). The intercept-only model was the top model for coyotes, indicating no relationship between the proportion of human modification within home ranges and home range size.

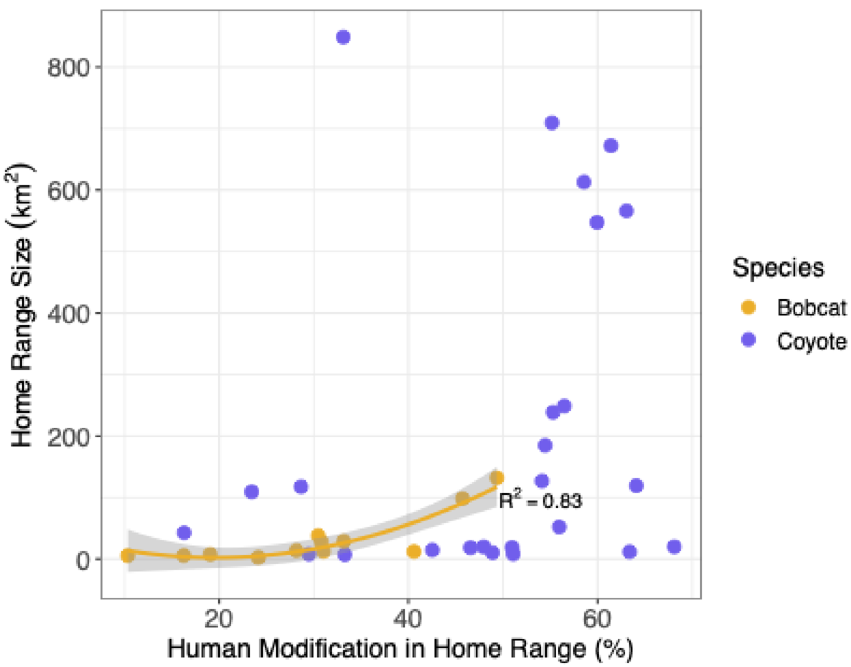

Figure 2. Individual bobcat and coyote home range size estimations paired with the proportion of human modification within the home ranges. Bobcat home range size had a quadratic relationship with human modification (trendline with R^2 value and confidence interval shadow shown), while coyote home range size had no relationship with human modification.

Resource Selection

Only one bobcat was tracked during the early winter season and fall night periods, so those periods were excluded from the bobcat RSF results (Supporting Information). Bobcats avoided agriculture during the spring/summer season, weakly avoided it during late winter, and selected it during fall (n =14, k-fold mean=0.61, range 0.21-0.93) (Figure 3). Bobcats did not respond to exurban habitat or human modification. Bobcats weakly avoided "other" habitat during the spring/summer and late winter seasons and strongly avoided it during the fall season. Bobcats either weakly avoided or did not respond to distance to water and either weakly selected or did not respond to distance to road, meaning they tended to select areas farther from roads and closer to water in periods when they had any response.

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Figure 3. Population-level bobcat RSF coefficients of agricultural landcover, exurban landcover, other landcover, human modification, distance to water, and distance to road covariates in reference to forested landcover with 95% confidence interval bars. The results are divided by ecological bobcat seasons (late winter, spring/summer, fall) and diel period (day, night, crepuscular) for coefficients representing eight temporal periods.

Coyotes generally avoided agriculture regardless of season, but the strength of avoidance varied by temporal period; coefficients were highest during the day, followed by crepuscular, and were lowest at night regardless of season (n =31, k-fold mean=0.66, range 0.23-0.96) (Figure 4). Coyotes generally avoided exurban habitat, increasing avoidance at night during all seasons. Avoidance was more marginal in some temporal periods than in others. Coyotes also generally avoided "other" habitats, with intensity of avoidance varying by temporal period. Coyote avoidance of most landcover categories during most temporal periods indicated they mainly preferred forest over alternative habitat types. Coyotes generally did not select for or avoid human modification. They generally selected areas closer to water and marginally selected for distance to road during most temporal periods.

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Figure 4. Population-level coyote RSF coefficients of agricultural landcover, exurban landcover, other landcover, human modification, distance to water, and distance to road covariates in reference to forested landcover with 95% confidence interval bars. The results are divided by ecological coyote seasons (early winter, late winter, spring, summer/fall) and diel period (day, night, crepuscular) for coefficients representing twelve temporal periods.

Impacts of Human Modification on Predator Behavior

Bobcats exposed to more human modification selected for more agriculture (Figure 5 upper row). This relationship was positive and quadratic in the mean of all temporal periods, quadratic in late winter, and linear during the spring/summer day temporal periods. There were also mostly positive quadratic relationships in the spring/summer day and night periods. Exurban selection and human modification exhibited a mean linear relationship and a negative linear relationship during the late winter season, indicating that bobcats avoided exurban habitat with increased human modification in late winter. Bobcats also exhibited negative linear trends in the relationship of human modification and distance to water in the mean, late winter, and spring/summer crepuscular periods, indicating selection closer to water with increased human modification.

Coyote selection for agriculture varied in response to human modification. Agriculture selection linearly increased in the mean and spring crepuscular and night periods and linearly decreased in the spring day period with increasing human modification (Figure 5 bottom row). There was no mean relationship between coyote selection for exurban habitat and human modification. However, there were two negative linear trends in the spring crepuscular and night periods, and a mostly positive quadratic relationship in the late winter crepuscular period. Coyote selection had a mean quadratic relationship between human modification and distance to water, which increased and then decreased, as well as slight linear negative trends in spring day, crepuscular, and night periods. There were stronger negative linear trends in the summer/fall crepuscular and night periods, and a negative quadratic trend in the summer/fall day period indicating that, in general, coyotes selected areas farther from water as human modification increased. Distance to road regressions yielded intercept-only top models for all temporal periods and means for both bobcats and coyotes, indicating no relationship between intensity of human modification and distance to road (Supporting Information).

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Figure 5. Top linear and quadratic regression model trendlines for bobcat (top row) and coyote (bottom row) functional responses. Individual-level RSF coefficients for agricultural landcover, exurban landcover, and distance to water were regressed against the response to the proportion of human modification present in each individual's home range. Trendlines are displayed for specific temporal periods (solid) or mean of all temporal periods (bolded and dashed). R^2values are displayed for each regression.

Discussion

Using a gradient of human modification within two study sites, we aimed to better understand how landcover types and intensity of human modification affect mesocarnivore movement behaviors both spatially and temporally, and where these behavioral responses can be found along the generic-to-nuanced gradient of response complexity. As hypothesized, we found drastic differences between bobcats and coyotes in the degree of complexity in their responses to human modification. While differences in wildlife species' response to human activity has been studied before (e.g., Frey et al. 2020), our work characterized specific responses to anthropogenic disturbances based on a variety of behaviors across spatial and temporal contexts. Generic bobcat responses included larger home ranges with increased human modification and weak selection responses to agriculture, exurban areas, and human modification. Bobcats also displayed functional responses in their resource selection choices that were relatively temporally consistent. In contrast, coyote nuanced responses included home range sizes that were unaffected by human modification, but displayed stronger avoidance of agriculture, exurban areas, and human modification than bobcats, indicating more fine-scale avoidance behaviors within the home range. Coyote resource selection functional responses were more nuanced, temporally-dependent, and sometimes changed direction depending on the amount of human modification. Our work provides evidence that species inhabiting the same landscape, and even filling a similar trophic role, can vary widely in the degree of nuance in their behavioral response to their environment. Specifically, our work shows the importance of investigating spatial and temporal variation in habitat selection and functional responses to better understand the complexity in how extrinsic factors shape wildlife behavior.

Predator Spatial Behavior and Response to Human Modification

While sex had no effect on bobcat home range size, study site did have a significant effect. Overall, increased levels of human modification within home range was correlated with larger home range size in bobcats. Bobcats tend to use larger home ranges in more fragmented and developed landscapes (Riley et al. 2003, Tucker et al. 2008) and lynx (*Lynx lynx*) have been found to expand their home ranges in order to increase hunting efforts in areas with declining prey abundance (Schmidt 2008). Therefore, the fragmentated, patchy landscape and increased human modification in the central Illinois site could be leading to low-quality forage for bobcats, causing them to expand their home ranges to maintain access to necessary resources (Reding et al. 2013, Nielsen et al. 2017). Coyotes had larger home ranges than bobcats, but a large amount of variation was present within the coyote population (Gese et al. 1988, Grinder and Krausman 2001). Sex and study site accounted for some of that observed variation, but neither had a significant effect on home range size. Other coyote populations have increased home range size with more forest cover (Ellington and Murray 2015), but coyote home ranges in this study were unaffected by the large difference in forest cover between the two study sites. In addition, there was no correlation between human modification within their home ranges and home range size in coyotes. This lack of response is likely due to coyotes adapting to human modification in their home ranges in other ways, such as spatial choices within their home ranges (Gehrt et al. 2009) or temporal adaptations to human activity (Gaynor et al. 2018, Shamoon et al. 2018).

Coyotes displayed a higher degree of temporal adjustment in their resource selection coefficients than bobcats; their responses were more varied depending on the temporal period, both diel and by season, than bobcats. We observed bobcat tolerance of human modification and exurban habitat regardless of temporal period, which was unexpected based on previous studies (e.g., Reed et al. 2017). Bobcats could be diluting the human density within their home ranges by expanding their home ranges in response to human modification, becoming less negatively affected by human modification and exurban areas overall. This dilution is possible as long as human use is below a certain intensity (Nielsen and Woolf 2001, Ordeñana et al. 2010).

Bobcats and coyotes both adjusted their responses to agriculture, exurban habitat, and water depending on the degree of human modification around them. Bobcat functional responses to human modification in their home ranges were straightforward, selecting more agriculture, less exurban habitat, and areas closer to water as human modification increased. This means that human modification does impact bobcat behavior, causing them to adjust their use of habitat accordingly, which was expected (Flores-Morales et al. 2019). The directionality of these trends was consistent when they were present regardless of the temporal period, although the strength of the trend sometimes varied by temporal period. Coyotes had a more varied response to human modification, and cumulative (mean) annual responses did not always reflect trends in individual temporal periods. In addition, regressions were sometimes quadratic and changed direction after a threshold of human modification. Overall, coyote functional responses to human modification were more nuanced and temporally-acute than those of bobcats.

Generic-to-Nuanced Gradient of Response to Anthropogenic Change

Taken altogether, these results support the idea that bobcats and coyotes are at different ends of the generic-to-nuanced response gradient. Bobcats exhibited a "broad-stroke", generic response to human modification. When faced with human modification, bobcats expanded their home ranges and functionally responded in their selection in a predictable manner with little temporal variation and complexity in their resource selection overall. These results corroborate previous work that shows that bobcats avoid humans (e.g., Reilly et al. 2022) and rely on corridors across a development gradient (Popescu et al. 2021, Mayer et al. 2022). In contrast, human modification did not affect coyote home range size, but it did cause coyotes to have more temporally-acute resource selection behaviors and varied and complex functional responses in their resource selection, which often changed temporally in intensity or direction. Compared to bobcats, coyotes were able to fine-tune their spatial behavior by avoiding the aspects of human modification that were disadvantageous on a finer scale within their home range instead of expanding their range. While it might be unanticipated that a species adapted to coexistence with humans would avoid human modification, this avoidance of human-associated areas (Gosselink et al. 2003) is a part of their adjustment strategy. Coyote temporal adjustments have been documented, including changing habitat preferences on a daily scale to avoid risk (Petroelje et al. 2021, Rivera et al. 2021) and on a seasonal scale to exploit seasonal resources (Webster et al. 2022). The overall nuance of coyote response to human modification illustrates how a species' response to novel environments can occur on multiple scales. These responses highlight differences in population-level plasticity between the two species.

Focusing on multiple aspects of space-use by investigating home-ranging behaviors and resource selection including spatial, temporal, and individual variation allowed us to reveal the complexity and differences in mesocarnivores' responses to anthropogenic disturbance. While investigating functional responses in resource selection is becoming more common (Godvik et al. 2009, Herfindal et al. 2009), investigating temporal variation in these functional responses is rarely done, yet considering this aspect is critical in understanding the degree of nuance in spatial behavior. However, using these characteristics allowed us to develop the generic-to-nuanced gradient, a framework where we can categorize species based on several spatial behaviors and highlight how a species is responding to anthropogenic change. Finding where a species or population falls along the generic-to-nuanced gradient described here can have important conservation and management implications. As human modification continues, understanding the full extent of its effects on wildlife population dynamics and fitness (Webber et al. 2020) as a result of individual- and population-level responses is increasingly crucial. Species that are less plastic are more likely to be disadvantaged in high-disturbance environments, while behavioral flexibility leads to increased success and tolerance of anthropogenic environments (Lowry et al. 2013, Lovell et al. 2022). For example, bobcat populations in North America only recently began recovering after record lows in the 1900's (Roberts and Crimmins 2010), while coyote populations have both increased in number and range across North America with anthropogenic land changes and extirpation of large predators (Linnell and Strand 2000, Laliberte and Ripple 2004), illustrating the implications of species-level plasticity and tolerance to human modification. However, while a nuanced response to human modification can provide benefits in exploiting anthropogenic habitat, there are also risks associated with this behavior. Forty-two percent of the coyotes in this study (n =13) were killed (hunted or trapped) within one year after being collared. While coyote abundance in this population appeared to remain stable despite these mortalities, it remains that there is a risk to individuals coexisting with humans.

The gradient of nuance in spatial response described here could be used as another metric to predict how species will react to future changes, and potentially as how best to manage them. Rettie and Messier (2000) proposed the "hierarchy of limiting factors" hypothesis, stating that species will display space-use response at a broader scale to address their most limiting factors. Similar to this idea, species on the generic end of the spectrum appear to respond to human development by displaying broad spatial response, indicating that habitat itself might be their biggest limiting factor (Rettie and Messier 2000). As such, managing species like bobcats should focus on habitat manipulation to mitigate blanket responses in home range size and habitat selection. Species on the nuanced end of the spectrum, like coyotes, may respond more to factors impacting the type of interactions with humans, such as harvest management, because they can be more flexible in habitat use and risk avoidance on a temporal scale. In such, our generic-to-nuanced framework highlights the importance of investigating spatial, temporal and individual responses to elucidate how other species might be impacted by human activities and how to best mitigate these activities.

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