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Influence of habitat structure and food on patch choice of captive coyotes

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ABSTRACT

Increasing urban development can have significant effects on wildlife species, including carnivores. Some carnivore species have been able to adapt to and even thrive in urban environments, including coyotes (*Canis latrans*). The presence of carnivores in urban areas can sometimes lead to conflicts with humans and their pets. Although coyotes may frequently use urban areas, they also inhabit natural areas surrounding urban development. Understanding the various factors affecting patch choice of urban coyotes may assist wildlife officials in managing human-coyote conflicts. Both sex and behavioral profile can influence patch choice; bold individuals are more likely to be exploratory than shy animals, which can result in increased conflicts in urban environments. Using a captive population of coyotes, we tested whether coyotes preferred urban (anthropogenic) habitat structure, natural structure, or a mixture of structures and whether sex, behavioral profile, biological season, or food manipulation affected coyote patch choice. Coyotes generally preferred the control, homogeneous structure representing their natal habitat (mean percentage of time 23.3% ± 19.3 SD; $P = 0.037$). The next most preferred habitat for coyotes, especially females (23.7 ± 16.6% for 25% urban pen; $P = 0.020$) and bold coyotes (27.8 ± 23.2% for 75% urban pen; $P = 0.005$), was a mixture of anthropogenic and natural structures rather than uniform structure (all natural or all anthropogenic), and this preference was more strongly expressed during the non-breeding season (25.6 ± 23.2% for 75% urban pen; $P = 0.017$). Food had no effect on patch choice ($P = 0.983$); coyotes appeared to be primarily motivated by the structure of the habitat rather than by the amount of food within each habitat. Our results suggested that urban areas containing large amounts of both natural and anthropogenic structures are more likely to be used by coyotes and, thus, could have the potential for human-coyote conflicts.

1. Introduction

Patch choice theory states an animal will choose the most profitable patch, or the patch containing the highest density of prey (Goss-Custard, 1977; Krebs et al., 1977; Stephens and Krebs, 1986). However, some studies contradict this theory, reporting that animals are willing to expend more energy even when food is freely available (Forkman, 1991; Inglis and Ferguson, 1986; MacLean et al., 2005). Inglis and Ferguson (1986) suggested animals are willing to spend more time and energy foraging in order to gather information about their environment, including knowledge of alternative food sources. This concept might apply to animals that are more certain of their survival

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(Forkman, 1991) or have certain behavioral profiles, such as boldness (Kurvers et al., 2012).

Studies have shown individuals within many animal species can have varying personalities, or behavioral profiles (i.e., more bold or more shy; Gosling, 2001; Sih et al., 2004). Bold individuals are more likely to be exploratory, and shy individuals may exhibit a greater degree of vigilance in unfamiliar situations (Wilson et al., 1993). Differences in behavioral profiles can affect animal movements, including the ability to find novel food sources (Fraser et al., 2001), and can influence patch choice. Patch choice decisions may vary between urban and natural systems because animals living in urban environments frequently display different behaviors than animals living in rural areas (Sol et al., 2013). Certain behavioral profiles, e.g., boldness, might be important in successful colonization of urban areas (Lowry et al., 2011).

Global landscapes are becoming increasingly urbanized, and the world's human population is now dominated by more individuals living in cities than in rural areas (Seto et al., 2012; United Nations Population Fund, 2007). Urban development significantly affects the natural environment and, therefore, many wildlife species (Mcdonald et al., 2008; McKinney, 2002). Several species are able to persist in urban environments, including those species previously associated only with rural or undeveloped landscapes (Ditchkoff et al., 2006), by modifying their behaviors (Tigas et al., 2002), habitat use (Prange et al., 2004), and foraging strategies (Fleischer et al., 2003). Certain carnivore species have also demonstrated an ability to adapt to and thrive in urban environments (Baruch-Mordo et al., 2008; Beier, 1995; Gehrt et al., 2009; Riley et al., 1998). Patch choice in carnivores can be influenced by both landscape structure and the availability of food resources in fragmented landscapes (Mortelliti and Boitani, 2008), although cost-benefit thresholds may be reached beyond which carnivores cannot use highly-urban, human-dominated patches (Baruch-Mordo et al., 2013).

Coyotes (*Canis latrans*) are highly adaptable, opportunistic carnivores and habitat generalists (Bekoff and Gese, 2003; Morey et al., 2007) and are increasingly colonizing urban areas (Gehrt et al., 2009; Grinder and Krausman, 2001). Coyotes living in close proximity to humans and their pets may cause conflicts, which have become an important consideration for urban wildlife managers (Gehrt et al., 2009; Lukasik and Alexander, 2011; Poessel et al., 2013). Although urban coyote diets are typically dominated by native small mammals, such as rodents and lagomorphs (Fedriani et al., 2001; Lukasik and Alexander, 2012; Morey et al., 2007), coyotes will sometimes take advantage of anthropogenic food sources associated with humans, placing them in increasing contact with humans and their pets (Gehrt and Riley, 2010). The availability and abundance of food may be an essential determinant of coyote habitat use (Knowlton et al., 1999; Morey et al., 2007; Turner et al., 2011). However, food may not always influence coyote spatial patterns. Alternative factors, including habitat features or denning sites, might be more important than food in determining space use in coyotes (Young et al., 2008).

Previous studies of space use in urban areas have shown coyotes select natural habitats within their home ranges and minimize exposure to human development (Atwood et al., 2004; Gehrt et al., 2009; Gese et al., 2012; Grinder and Krausman, 2001; Quinn, 1997; Riley et al., 2003). Hence, although coyotes may use urban areas, they generally utilize natural areas integrated into or surrounding urban development. Understanding the factors influencing a coyote's decision regarding patch choice could prove beneficial in managing human-coyote conflicts in urban areas and predicting coyote behavior related to space use.

Our objective was to determine which factors, including sex, behavioral profile, and biological season, affected coyote patch choice along a gradient from natural to urban habitat structure, and how manipulation of the quantity of food might guide coyote decision-making. We defined habitat as the resources necessary for an animal to survive; however, we only manipulated food and the structure within the habitat. We used captive coyotes, maintained for research purposes, to experimentally test these factors. We hypothesized that bold coyotes would use urban patches more than shy coyotes, and that food availability would affect coyote patch choice more than habitat type.

2. Materials and methods

2.1. Study site

We conducted the study at the USDA/National Wildlife Research Center (NWRC) Predator Research Station in Millville, UT, USA, which houses a large population of coyotes maintained individually and in pairs. For this study, we used an interaction pen system consisting of one center pen and six pens (each pen 0.1 ha measuring approximately 40 m across at the widest point) surrounding and attached to the center pen by fenced alleys with gates at each end of the alleys (Fig. 1); the topography was flat. Each of the six outer pens contained a den box (0.5 m high × 0.5 m diameter) with corn cob bedding (Green Products Company, Conrad, IA, USA), an automatic water source, and a 0.7 m high wooden shade table, which were standard items placed in all coyote pens at the facility. The center pen consisted of native grasses, i.e., native habitat, but no additional structures or plants; this habitat was similar to the environment in which coyotes at the facility were raised. Five of the six outer pens were designed to simulate a gradient of habitat structure from planted shrubs and trees (defined as "natural") to anthropogenic structures (defined as "urban"); the coyotes at the facility were unfamiliar with these types of habitat structures. The sixth outer pen remained similar to the center pen and acted as the experimental control pen (hereafter "control"). One pen was designated as all natural (hereafter "0% urban") and included structurally native vegetation (i.e., shrubs and trees) planted before study commencement. Another pen was designated as all urban (hereafter "100% urban) and included anthropogenic structures made from plywood and wood pallets, trash cans, a culvert, and solar lights placed on top of certain wooden structures. The remaining three pens included a mixture of natural vegetation and urban structures, with one pen containing 25% urban and

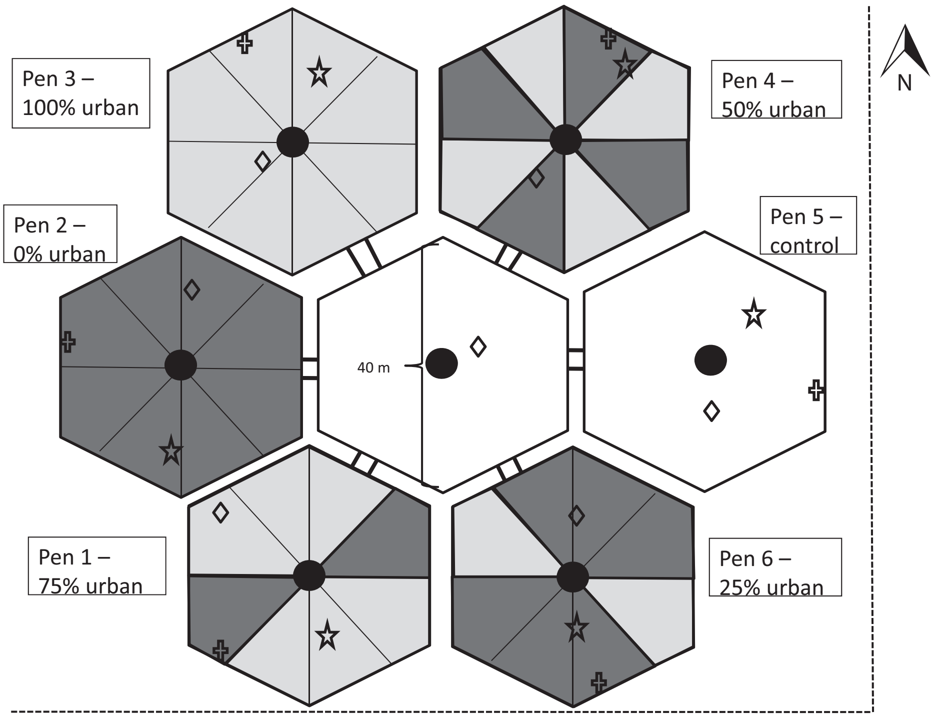

Fig. 1. Diagram of the interaction pen system at the USDA-WS-National Wildlife Research Center Predator Research Station. Each of five pens was divided into eight sections: urban sections (in light gray shading) included wooden structures and natural sections (in dark gray shading) included four plants. Two pens were left in an unmanipulated state. The dark circle represents where food was placed, the cross represents the placement of the watering system, the diamond represents the placement of the den, and the star represents the placement of the shade table in each pen. The dimension of a pen at its widest point is included on the center pen. The dashed line indicates the approximate location of the fence.

75% natural structural habitat (hereafter "25% urban"), one pen with 50% urban and 50% natural structural habitat (hereafter "50% urban"), and one pen including 75% urban and 25% natural structural habitat (hereafter "75% urban"). We randomly chose which of the six pens would receive each habitat design before study commencement. Due to the complexity of our habitat design, we were unable to randomly reallocate habitat structure to each pen before testing each study animal; thus, each pen retained its original habitat structure throughout the duration of the study. This constant habitat design, where each type of habitat structure remained in the same location, might have influenced the pen choices of our study coyotes. We also built a fence covered with black shade cloth (approximately 1.5 m tall) surrounding two sides of the interaction pen system (at least 15 m away from the pens) to block the view of study coyotes from other coyotes at the facility. This fence was built after the first two animals tested were observed interacting with coyotes in neighboring pens. We included these two animals in our data analysis because their results were similar to the results for animals tested after the fence was built (i.e., preferred mixed habitat pens over uniform pens, although we did not analyze these data statistically). Finally, we placed a traffic counter (TrailMaster®, Goodson & Associates, Inc., Lenexa, KS, USA) at the entrance to each of the six outer pens to determine when a coyote entered or exited each pen. Each unit consisted of a receiver and transmitter with an invisible active infrared beam between them, and the receiver recorded the date and time the infrared beam was broken by a coyote. This system allowed us to determine the amount of time spent in a pen by calculating the difference between entrance and exit times. Study animals were fed a ground meat, commercial diet (Fur Breeders Agricultural Cooperative, Logan, UT, USA) which we froze into food balls. Water was provided *ad lib* in all six outer pens via an automatic watering system. Monthly temperatures at the study site ranged from a mean low of $-11\,^{\circ}$C in December to a mean high of $33\,^{\circ}$C in July.

2.2. Study design

We tested a total of 24 coyotes individually. We chose an equal number (six) of coyotes from the following categories: bold males, bold females, shy males, and shy females. We determined bold versus shy coyotes from video recordings of each coyote being exposed to a plastic coyote model placed in their pens before this study began. We categorized coyotes that quickly approached the model as bold (mean latency to approach 1:05 min $\pm$ 0:38 SD) and those that avoided it as shy (never fully approached the model), based on the definition of bold individuals as showing exploratory tendencies and shy individuals as retreating from unfamiliar situations (Wilson et al., 1993). By including boldness/shyness as a factor in the study, we could examine the variability in patch choice due to behavioral or personality differences. All coyotes were $\geq$1.5 years of age. We tested three of the six coyotes in each group during the breeding season (November to April) and three during the non-breeding season (June to October). Order of testing was based on the availability of individual coyotes, but predominantly followed the pattern of shy female, bold male, bold female, and shy male.

We tested each coyote for 8 days. For the first 4 days we tested coyote patch choice based on habitat structure only, and for the next 4 days we tested patch choice based on both habitat structure and food. Because coyotes at the facility generally tend to eat their food quickly, we determined that 4 days was sufficient time to detect any changes in coyote patch choice based on food. We placed each coyote in the center pen on the first day, allowing free access to all of the pens. For the first 4 days, we fed the study animal 800 g of food in the center pen; this amount was similar to the amount of food all coyotes at the facility are given on a daily basis. Towards the end of day 4, we downloaded and analyzed the data from the six counters to determine the percentage of use within each of the six outer pens, calculated by dividing the amount of time the coyote spent in each pen by the total amount of time the coyote spent in the six outer pens. On days 5–8, to determine whether food could modify the coyote's patch choices, we partitioned 1575 g of food throughout the six outer pens on a decreasing scale based on an increasing percentage of use of the pens during days 1–4. For example, we placed the highest amount of food in the pen used the least percentage of time, and the lowest amount of food in the pen used the most. We divided the 1575 g of food as follows among the six pens: 800, 400, 200, 100, 50, and 25 g, effectively doubling the amount of food in each pen from most-used to least-used pen. We closed the coyote in the center pen while the food was distributed among the six pens each day, then opened the gates to all of the pens at the same time, allowing the coyote access to all pens. At the end of day 8, we removed the coyote from the interaction pen system and downloaded and analyzed the data from the counters for days 5–8. We then cleaned the pens (i.e., removed scats) over the next 1–2 days and readied them for the next study animal.

We conducted observations on 14 (three bold females, four shy females, four bold males, three shy males) of the 24 coyotes to determine microhabitat use within the mixed structure pens. During the first 4 days a coyote was in the interaction pen system (when we tested coyote patch choice based on habitat structure only), we observed the study animal four times per day for 5 min. When the coyote entered one of the mixed habitat pens (i.e., 25% urban, 50% urban, or 75% urban pens), we recorded which habitat, urban or natural, the coyote used. Habitat use was defined as a coyote being located within one of the eight sections of a pen (see Fig. 1). Resources placed in each pen (i.e., water, dens, and shade tables) were rarely used by coyotes during our observations and, thus, did not influence microhabitat use. Certain microhabitats of the same type (urban or natural) were, by design, adjacent in the 75% urban and 25% urban pens, which could have influenced coyote use. At the end of the first 4 days, we summed the number of times each coyote used urban habitats and natural habitats while in the three pens, and we then calculated the proportion of times each coyote used each habitat in these pens. Animal handling protocols were approved by the Institutional Animal Care and Use Committee at the National Wildlife Research Center (QA-1931).

2.3. Statistical analyses

We used data from the traffic counters to determine patch choice, measured as percentage of time spent in each of the six outer pens. Because our data were compositional, i.e., the percentages of time spent in each pen summed to 100%, we transformed the percentage of time response variable with a log-ratio transformation (Aitchison, 1986), using the percentage of time in the control pen as the reference level. Thus, the transformed response variable consisted of dividing the percentage of time in each of the 0% urban, 25% urban, 50% urban, 75% urban, and 100% urban pens by the percentage of time in the control pen, then taking the log of each ratio. We assessed the effects on the response variable by using a linear mixed model with the coyote as a random-effects factor associated with the fixed-effects factors sex (female/male), behavioral profile (bold/shy), and biological season (breeding/non-breeding). Repeated measurements on a coyote was a random-effects factor associated with the fixed-effects factor food manipulation (before/after), and multiple observations on each coyote within each food manipulation trial was a random-effects factor associated with the fixed-effects factor pen. We also analyzed all two-way and three-way interactions among the various factors. We used an unstructured matrix to model the covariance structure for the multiple pen observations, which is analogous to a multivariate analysis of variance. We estimated denominator degrees of freedom using the Kenward–Roger method. For any significant interactions or main effects, we analyzed specific pairwise comparisons of interest with t-tests, correcting P-values with a Tukey adjustment. Only adjusted P-values that were significant are reported.

For the microhabitat data collected from the 14 observed coyotes, we conducted a chi-square test comparing the average percentage of time coyotes used urban and natural habitats while in the mixed pens with the expected percentage of time, based on availability of 50% each. We also ran a non-parametric Kruskal–Wallis test with the observed percentage of time spent in urban habitats while in the mixed pens as the response variable and sex and behavioral profile as predictor variables. We set the significance level to 0.05 for all statistical tests, which were two-tailed. We used SAS v.9.3 for all statistical analyses (SAS Institute Inc., 2011).

3. Results

All coyotes, on average, preferred the control pen (mean percentage of time 23.3% ± 19.3 SD) throughout the study, followed by the 25% urban (18.2 ± 18.0%) and 75% urban (18.3 ± 19.4%) pens, the 50% urban (15.8 ± 17.4%) pen, and the 0% urban (13.6 ± 17.9%) and 100% urban (10.7 ± 13.1%) pens. When coyotes began using the interaction pen system after release, the known mean percentage of total experiment time spent in the center pen was 6.6 ± 2.3%. Because we were only interested in coyote patch choice of the six

Table 1
Tests of main effects and interactions for the model analyzing percentage of time coyotes spent in each of six pens, 2011–2012.

Effect[a]	Numerator *df*	Denominator *df*	*F*	*P*-value[b]
Sex	1	31	1.23	0.276
Personality	1	31	0.66	0.423
Sex * Personality	1	31	0.05	0.832
Season	1	31	5.59	**0.025**
Sex * Season	1	31	1.96	0.171
Personality * Season	1	31	0.37	0.547
Sex * Personality * Season	1	15	0.62	0.442
Food	1	22	1.02	0.324
Sex * Food	1	22	0.40	0.534
Personality * Food	1	22	0.02	0.894
Sex * Personality * Food	1	16	4.81	**0.044**
Season * Food	1	22	0.04	0.837
Sex * Season * Food	1	16	2.61	0.126
Personality * Season * Food	1	16	1.04	0.322
Pen	4	34	2.88	**0.037**
Sex * Pen	4	34	3.37	**0.020**
Personality * Pen	4	34	4.54	**0.005**
Sex * Personality * Pen	4	34	3.97	**0.010**
Season * Pen	4	34	3.49	**0.017**
Sex * Season * Pen	4	34	1.15	0.349
Personality * Season * Pen	4	34	0.85	0.501
Food * Pen	4	34	0.09	0.983
Sex * Food * Pen	4	34	0.26	0.901
Personality * Food * Pen	4	34	0.66	0.626
Season * Food * Pen	4	34	0.18	0.947

[a] Predictor variables for the model included sex of coyotes, either male or female (Sex), behavioral profile of coyotes, either bold or shy (Personality), season, either breeding or non-breeding (Season), before or after food manipulation (Food), pen number (Pen), and interactions among these variables.
[b] Bold denotes significance at the 0.05 level.

designed pens, and because the center pen was primarily used by coyotes as a funnel between the outer pens, we did not consider center pen usage further. Females and males differed in pen choice (Table 1, Sex * Pen interaction), as did bold and shy coyotes (Table 1, Personality * Pen interaction). Coyote patch choice also differed between the two seasons (Table 1, Season * Pen interaction). Percentage of time spent in each pen also varied within sexes and behavioral profiles, pooled across both seasons (Table 1, Sex * Personality * Pen interaction). One additional interaction, Sex * Personality * Food, was significant (Table 1); however, we did not consider this interaction further because we were only interested in the percentage of time coyotes spent among the different pens, and this interaction did not include Pen. No other interactions were significant, including any of those with Pen and Food.

Results for each pen are reported relative to the control pen. Percentage of time in the 75% urban (18.3 ± 19.4%) pen was higher than in the 0% urban (13.6 ± 17.9%) pen for all coyotes ($t_{37}=2.89$, $P=0.049$). Males preferred the 100% urban pen more than females ($t_{35}=2.31$, $P=0.027$; Fig. 2). Females preferred the 75% urban pen over both the 0% urban and 100% urban pens (0% urban: $t_{37}=3.67$, $P=0.007$; 100% urban: $t_{37}=3.05$, $P=0.033$; Fig. 2), and they also preferred the 25% urban pen over both the 0% urban and 100% urban pens (0% urban: $t_{37}=4.17$, $P=0.002$; 100% urban: $t_{37}=4.32$, $P=0.001$; Fig. 2). Males did not show any preference among pens.

Bold coyotes chose the 75% urban pen more than shy coyotes ($t_{32}=2.44$, $P=0.020$; Fig. 3). Bold animals chose the 75% urban pen more than both the 0% urban and 100% urban pens (0% urban: $t_{37}=3.59$, $P=0.009$; 100% urban: $t_{37}=3.33$, $P=0.017$; Fig. 3), whereas shy animals preferred the 25% urban pen over the 75% urban pen ($t_{37}=3.11$, $P=0.029$; Fig. 3).

Coyotes in the non-breeding season preferred the 75% urban pen more than coyotes in the breeding season ($t_{32}=3.55$, $P=0.001$; Fig. 4). Coyotes in the non-breeding season also preferred the 75% urban pen over both the 0% urban and 100% urban pens (0% urban: $t_{37}=3.26$, $P=0.020$; 100% urban: $t_{37}=3.20$, $P=0.023$; Fig. 4). Coyotes in the breeding season did not show any preference among pens.

Bold female coyotes chose the 75% urban pen more than the 0% urban pen ($t_{37}=3.64$, $P=0.008$; Fig. 5), and bold male coyotes chose the 75% urban pen more than the 25% urban pen ($t_{37}=3.52$, $P=0.010$; Fig. 5). Shy female coyotes preferred the 25% urban pen over both the 0% urban and 100% urban pens (0% urban: $t_{37}=3.25$, $P=0.020$; 100% urban: $t_{37}=3.95$, $P=0.003$; Fig. 5), and they also preferred the 50% urban pen over the 100% urban pen ($t_{37}=3.93$, $P=0.003$; Fig. 5). Shy male coyotes preferred the 100% urban pen more than shy female coyotes ($t_{35}=2.76$, $P=0.009$; Fig. 5). No differences in pen choice occurred between behavioral profiles within a sex.

For the microhabitat data, coyotes in the mixed habitat pens used urban habitats 51% of the time and natural habitats 49% of the time, which was proportional to availability ($\chi_1{}^2=0.03$, $P=0.853$). The percentage of time coyotes spent in urban habitats within each mixed pen was not affected by sex or behavioral profile ($H_3=1.64$, $P=0.651$).

4. Discussion

Habitat contains multiple components, including food and water resources, cover, and denning sites. In this study, we modified two components, the structure of the

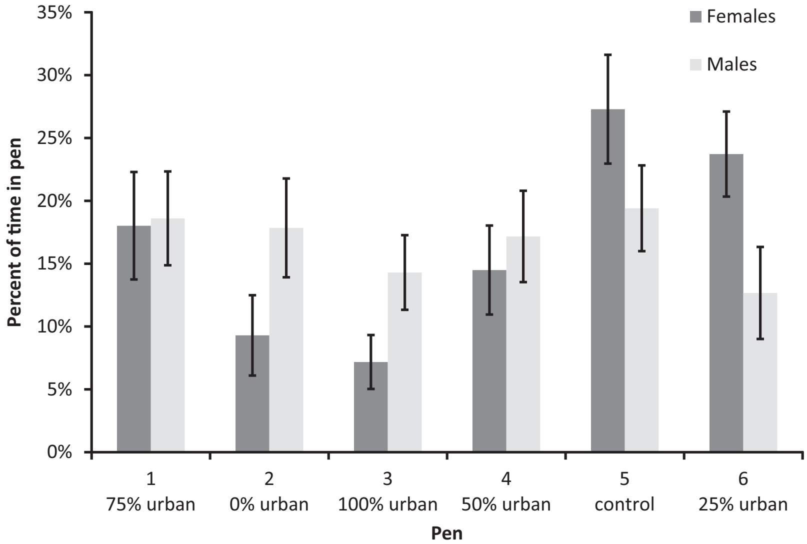

Fig. 2. Percentage of time spent in each pen by female and male coyotes. Bars represent standard error around the mean. Means and SEs are computed as descriptive statistics on the raw data and are not equal to those that are estimated and compared by the linear mixed model used to analyze the data.

habitat and food, to evaluate their effects on patch choice by coyotes. Coyotes generally preferred the control pen, then the pens with a mix of natural and urban habitat structure, over the pens with 0% urban or 100% urban habitat structure. Because the control pen consisted of similar habitat in which captive coyotes at the predator research facility are raised, our results support the idea that coyotes imprint on their natal environment (Gantz and Knowlton, 2005). Our results also indicated that coyotes, when investigating novel environments, prefer using heterogeneous habitats. Observations revealed that, when coyotes were in the mixed habitat pens, they used habitat according to availability, i.e., the percentage of time spent in urban and natural habitats within these pens was equal to the percentage of each habitat structure that was available. Such a habitat mixture is often preferred by wild coyotes, including urban coyotes (Rashleigh et al., 2008). Riley et al. (2003) found that only 10% of coyotes they studied had no non-natural area within their home ranges. Similarly, Gehrt et al. (2009) determined that only 8% of coyotes had no natural area (i.e., less-developed areas) within their home ranges, indicating coyotes usually select habitats containing natural areas with less human use and more cover.

Both female coyotes and bold coyotes followed the same general pattern in pen preference, choosing pens with a mixture of structure over pens with uniform structure. Shy female coyotes exhibited similar preferences, indicating that our overall results were most strongly expressed in

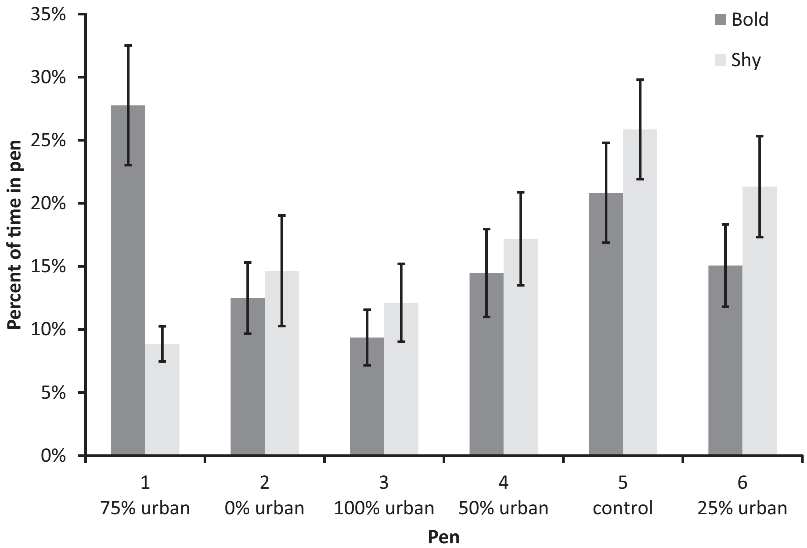

Fig. 3. Percentage of time spent in each pen by bold and shy coyotes. Bars represent standard error around the mean. Means and SEs are computed as descriptive statistics on the raw data and are not equal to those that are estimated and compared by the linear mixed model used to analyze the data.

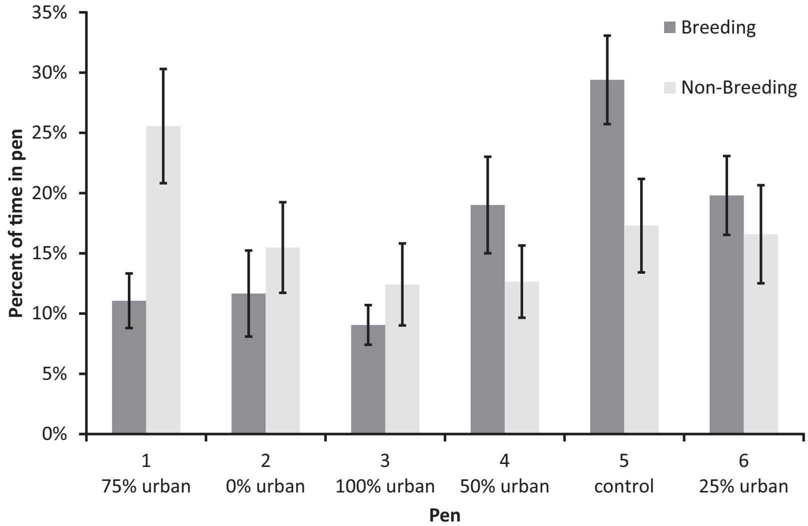

Fig. 4. Percentage of time spent in each pen by coyotes during the breeding and non-breeding seasons. Bars represent standard error around the mean. Means and SEs are computed as descriptive statistics on the raw data and are not equal to those that are estimated and compared by the linear mixed model used to analyze the data.

females. Grinder and Krausman (2001) determined home ranges of females followed the overall trend in habitat selection for coyotes in their study, in that home ranges included a smaller proportion of natural areas and a larger proportion of residential areas than were available in the study area. These results suggest females exhibit strong preferences which might drive habitat selection and patch choice in coyotes, whereas the preferences of male coyotes, which may follow females rather than habitat, might be more equivocal and less likely to influence overall patterns.

Bold coyotes also preferred one of the mixed pens (75% urban pen) over the homogenous pens and chose this pen more than did shy coyotes. Few studies have been conducted measuring boldness in coyotes; however, such studies have been performed on other species. Mettke-Hofmann et al. (2002) measured exploratory behavior (i.e., boldness) in 61 parrot species (*Psittaciformes*) and determined species that were more exploratory inhabited more complex habitats, including forest edges with a rich variety of vegetation. Evans et al. (2010) investigated boldness in urban and rural song sparrows (*Melospiza melodia*) and found urban birds were bolder towards humans than rural birds and showed higher levels of territorial aggression. Our results suggested bold coyotes might be more exploratory than shy coyotes, preferring the more complex habitats of the mixed pens, possibly because of the rich environment provided by habitat edges including large amounts of structural cover. In the context of patch choice theory, bold animals also may be more likely to explore heterogeneous patches to obtain information on alternative food sources.

Coyotes in the non-breeding season selected the 75% urban pen more than the uniform pens, and they also chose this pen more than did the coyotes in the breeding season. Because of courtship behaviors displayed by breeding coyotes (Bekoff, 1977), we might expect solitary coyotes during the breeding season to seek habitats located near other coyotes. At the NWRC facility, the mixed habitat pens (25% urban and 75% urban pens) were located closest to other coyotes. However, coyotes tested during the breeding season did not choose these pens as often as the coyotes tested during the non-breeding season. Hence, the proximity of conspecifics likely was not the reason our study animals preferred the mixed pens. Hernández and Laundré (2003) found coyotes used a greater diversity of habitat types during the pup-rearing season (coinciding with the non-breeding season in our study) but concentrated their activities in a single habitat type during gestation (coinciding with our breeding season), consistent with our results. They linked these differences in habitat use to changes in behavior between the two seasons. For example, coyotes do not travel far from den sites while raising pups when both the adult female and pups need to be provisioned with food (Harrison and Gilbert, 1985), so perhaps using a variety of habitat types increases the amount of food found within a smaller area. However, coyotes in their study also used a variety of habitats during pair formation, which also coincided with our breeding season and contradicted our results. Perhaps our delineation of breeding and non-breeding seasons was too coarse to detect fine-scale differences in patch choice through a coyote's biological seasons; instead we only found distinct differences between the breeding and non-breeding periods.

Food had no effect on coyote patch choice. Once coyotes selected a pen, they continued to use that pen even when more food was placed in less preferred pens. Observations indicated the coyotes readily brought food from the pens they did not prefer into the pens they did prefer. Hence, our results were inconsistent with patch choice theory because coyotes did not choose the most profitable patch, i.e., the pen with the highest amount of food, but instead chose patches based on some other factor, most likely habitat structure. Wild urban coyote populations are believed to exist at higher densities than those in nonurban areas

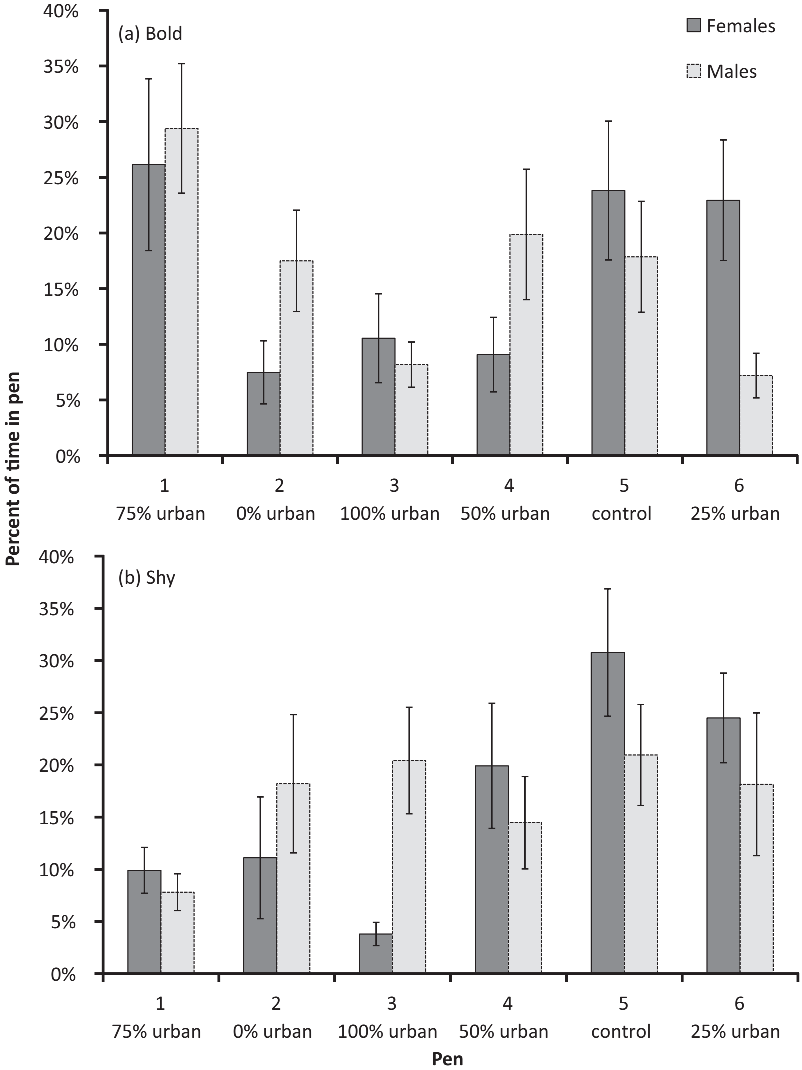

Fig. 5. Percentage of time spent in each pen by (a) bold and (b) shy female and male coyotes. Bars represent standard error around the mean. Means and SEs are computed as descriptive statistics on the raw data and are not equal to those that are estimated and compared by the linear mixed model used to analyze the data.

at least partially because of the abundant food resources found in urban environments (Fedriani et al., 2001; Gehrt and Riley, 2010; Quinn, 1997). However, our results suggest wild coyotes may choose urban areas for reasons other than food availability. Wild urban coyotes generally use a variety of urban environments, but their diet primarily consists of native foods (e.g., rodents) rather than anthropogenic foods found in urban landscapes (Morey et al., 2007). Hence, urban coyotes may identify attractive habitat patches containing food resources, and then reside in adjacent patches that meet other criteria, such as structural cover.

Several factors may confound the application of our results to wild coyotes. First, the captive coyotes in our study could easily carry food from one habitat patch to another, a choice not always available to wild coyotes occupying larger areas. Second, we approximately doubled the amount of food given to coyotes on days 5–8; if the coyotes had received less food, we may have seen different results, i.e., they may have been more food-motivated in their habitat choices. Finally, coyotes in captivity are more likely to have settled into a daily routine where they are fed by humans on a regular basis. Foraging is a small part of a captive coyote's activity budget, comparable to wild coyotes that may spend as little as 4% of their time on foraging (Gese et al., 1996). Hence, food may not be a principal motivator in the decision-making of a captive coyote, similar to the findings of Young et al. (2008) for wild coyotes. Additionally, our findings that patch choice theory did not apply to our captive study animals do not undermine its importance in wild coyotes; additional testing in free-ranging coyotes would be necessary to examine this theory where resident coyote home ranges (averaging from <1 km^2 [Young et al., 2006] to 121 km^2 [Boisjoly et al., 2010]) can be much larger than in captivity. Nevertheless, our results suggest coyotes primarily select habitat based on the structure of such habitat rather than food, especially when food can be easily transferred to a preferred habitat.

Habitat structure can affect the expression of certain behaviors by coyotes. Wilson et al. (2012) determined that the mesic-meadows habitat was selected by coyotes when foraging, but this habitat type had no influence on selection when generalized across all behaviors. Studies on other captive vertebrate species have noted the importance of habitat structure. Tiebout and Anderson (2001) found Florida scrub lizards (*Sceloporus woodi*) preferred sandy habitat types over habitats containing coarse woody debris which are likely too warm and thermally stressful and, therefore, impede lizard movement. Similar to our results for female coyotes, habitat preferences were expressed more strongly in female lizards than in male lizards (Tiebout and Anderson, 2001). Martinez et al. (2010) determined common redstarts (*Phoenicurus phoenicurus*) preferred habitats with sparse vegetation over dense meadows, even with a four-fold increase of food abundance in meadows. These findings demonstrated that habitat structure was more important than food for common redstarts (Martinez et al., 2010), comparable to our results for coyotes.

Our results should assist wildlife officials in North America in managing their urban coyote populations. Managers should be aware that urban areas incorporating large tracts of natural lands or open space interspersed throughout the urban matrix may be more likely to be used by coyotes and, as a result, have greater potential for human-coyote conflicts. The availability of abundant food resources in urban areas is considered to be a principal attractant of coyotes to urban environments (Fedriani et al., 2001; Gehrt and Riley, 2010; Grinder and Krausman, 2001; Quinn, 1997). However, our findings show that, at least in some cases, coyotes may be primarily motivated by the structure of the habitat and the amount of the habitat that consists of urban versus natural lands. Hence, managing the availability of complex habitats in urban areas may warrant further consideration by urban managers. Understanding that coyote behaviors can vary greatly based on sex and personality traits should also help urban managers in mitigating conflicts by implementing specific tools that target certain individuals. We found bold coyotes had clearer patch choices than shy coyotes. Home ranges of coyotes residing in developed areas may contain large amounts of urban lands, requiring coyotes to travel through a matrix of urban and nonurban landscapes, thus facilitating increased encounters with humans and their pets (Gese et al., 2012). The exploratory behaviors of bold coyotes might lead to increased aggression and conflicts with humans during such encounters (Evans et al., 2010). Identifying and focusing management efforts on bold individuals in urban areas might reduce the prevalence of conflicts. Urban wildlife officials, as well as citizens, should appreciate that coyotes are individualistic and can express a variety of behaviors and choices, including choice of habitat.

In conclusion, coyotes preferred pens with a mixture of both urban and natural structural habitats rather than pens with uniform structural habitats. This overall pattern in patch choice was most strongly expressed in females, bold coyotes, and coyotes in the non-breeding season. Contrary to our predictions, food had no influence on coyote patch choice; instead, coyotes chose pens based solely on habitat structure. These results, as well as results from future studies focused on managing individual coyotes with specific personality traits, should assist urban wildlife officials in managing their coyotes and mitigating human-wildlife conflicts.

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