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Coyote (*Canis latrans*) Habitat Selection in Urban Areas of Western Washington via Analysis of Routine Movements

Abstract

Habitat preference is often determined by examining temporally independent animal location data with little attention paid to movement behavior. In 1989 - 90, I examined coyote habitat preference in urban areas of Washington State by examining habitat used by 6 radio-collared coyotes during routine movements. I represented routine movements as straight lines connecting consecutive radio-relocations taken at 1-hour intervals during a series of 6-hour tracking sessions. I used compositional analysis to determine if coyotes selected for particular habitat types at 2 spatial scales: i) home range from within an arbitrarily defined study area containing all home ranges and ii) areas used during routine movements from within the home range. There was no difference ($P = 0.631$) in habitat composition between the home ranges and the study area. However, based on habitat availability in home ranges, coyotes preferred ($P < 0.036$) Forest = Shrub > Densely mixed vegetation > Moderately mixed vegetation > Sparsely mixed vegetation during routine movements.

I used stepwise multiple regression to explore the relationship between movement distance and quality of habitat in which the movement began (initial habitat), habitat in which the movement ended (final habitat), habitat gradient (initial - final habitat), and light conditions (night vs. day). Light conditions ($P = 0.006$) and the interaction of light and initial habitat ($P = 0.004$) were significant but weak predictors (multiple $R^2 = 0.137$) of movement distance. Coyotes moved longer distances at night than during the day. Movement distance tended to increase with decreasing habitat quality at night but showed little relationship with habitat quality during the day. Coyotes preferred to travel through, and remain in close proximity to, relatively undisturbed (Forest and Shrub) habitats in urban environments of Washington State.

Introduction

Urbanization dramatically alters natural landscapes and frequently results in a mosaic of small habitat fragments which themselves vary in their degree of disturbance. Perhaps the most obvious change accompanying urbanization is the decrease in the amount of natural vegetation. The largest remaining patches of natural vegetation are typically associated with parks and reserves and often constitute important habitat for mammalian wildlife (Harris 1977, Harris and Rayner 1986). For example, Dickman (1987) recorded as many as 17 species of mammals using small woodland patches in Oxford, England and further showed that species richness in these patches was negatively correlated with several measures of disturbance. However, often it is not clear what role these fragments of vegetation play in the maintenance of urban wildlife populations. In addition, few studies have looked at the way wildlife species use these areas.

The coyote (*Canis latrans*) is a common inhabitant of cities throughout the United States and is often associated with patches of natural vegetation (Gill and Bonnett 1973, Quinn 1995). Urban environments offer a unique opportunity to explore aspects of coyote behavior. For example, does the coyote represent a species that has changed its behavior to exploit urbanized habitat or is it simply a species clinging to remnant patches of natural habitat?

Many studies have explored coyote habitat use patterns by examining temporally independent radio-locations. However, the use of independent observations may limit the type of inference that can be made about coyote behavior because it fails to document how and why animals use an area (Sanderson 1966, Laundré and Keller 1984). Using sequential radio-telemetry data, Laundré and Keller (1981) were able to identify three types of coyote movement patterns that represented three general types of behavior: resting, hunting, and

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traveling behavior. Although Laundré and Keller (1981) did not explicitly study the effect of habitat type on movement behavior, they postulated that specific movement patterns were associated with unique vegetal, faunal, or physiographic characteristics of the home range. To my knowledge there are no studies that have looked at habitat use during routine movements of coyotes where routine movements were defined as movements other than dispersal. The purpose of this study was to explore the relationship between coyote movements and habitat patterns in urban environments.

Methods and Materials

Study Area

The study area was the low elevation (<100 m), portion of King County, Washington (Figure 1). This part of Washington State lies in the wetter region of the Western Hemlock Zone (Franklin and Dryness 1984). Although most of the forest area has been cleared for urban expansion, there are numerous small patches of 40-80-year-old forest consisting primarily of Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), red alder (*Alnus rubra*), big leaf maple (*Acer macrophyllum*), and vine maple (*Acer circinatum*) (Franklin and Dyrness 1984).

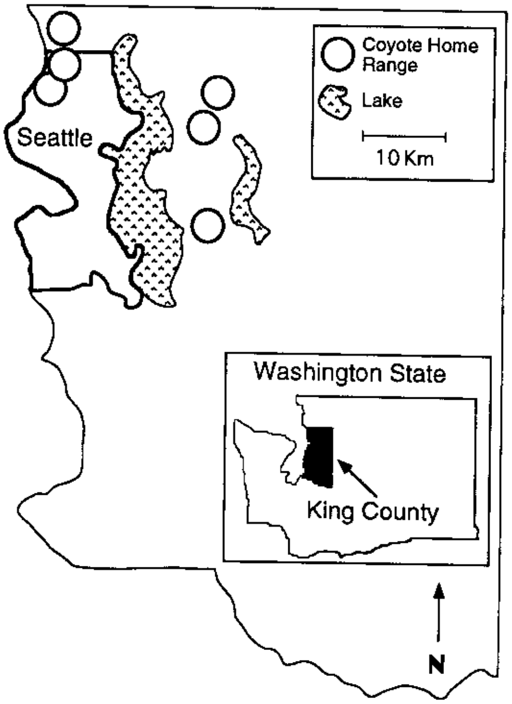

Figure 1. Location of the radio-telemetry study area in the greater Seattle metropolitan area, King County, Washington, 1989-90. The study area was defined as the smallest area containing all coyote relocations. Circles show approximate location of coyote home ranges.

Radio Telemetry

I captured 6 (3 M, 3 F) adult (>1 year old) coyotes using Victor #3 traps with padded jaws during 1989-90. I captured coyotes in the greater Seattle metropolitan area; 3 within 1 km of Seattle's northern border, whose home ranges included part of Seattle, and 3 in urban environments adjacent to Seattle (Figure 1). Each coyote was fitted with a radio transmitter and released at the capture site. During 1990, I followed each coyote during 12, 6-hour, tracking sessions in each of 4 seasons, breeding (1 Jan - 15 Mar), gestation (16 Mar - 30 Apr), pup-rearing (1 May - 31 Jul), and dispersal (1 Aug - 31 Dec). Tracking sessions started at 0600, 1200, 1800, or 2400 with 3 sessions/time period. Consecutive tracking sessions for an individual were separated by ≥24 hours and were typically spaced evenly throughout the season. I located coyotes at 1-hour intervals during a tracking session resulting in 6 locations and 5 movements. I represented movements as straight lines connecting consecutive locations and movement time as the hour the movement was completed (Figure 2). I designated daylight (day) movements as those occurring from 0700-1700 for breeding season, 0700-1900 for gestation season, 0600-2100 for pup-rearing season, and 0700-1900 for dispersal season. All other movements were considered night movements.

Clearly, characterizing coyote movements as straight lines between radio-locations at 1-hour intervals is a simplification that could affect the validity of my study. However, I believe my study approach was appropriate for three reasons. First, I had to chose a time interval to characterize movements that would be long enough to allow an animal to move across a number of pixels so that proportions for *used* and *available* habitat could be calculated, but not so long as to completely obscure important aspects of behavior related to general (all behaviors combined) use

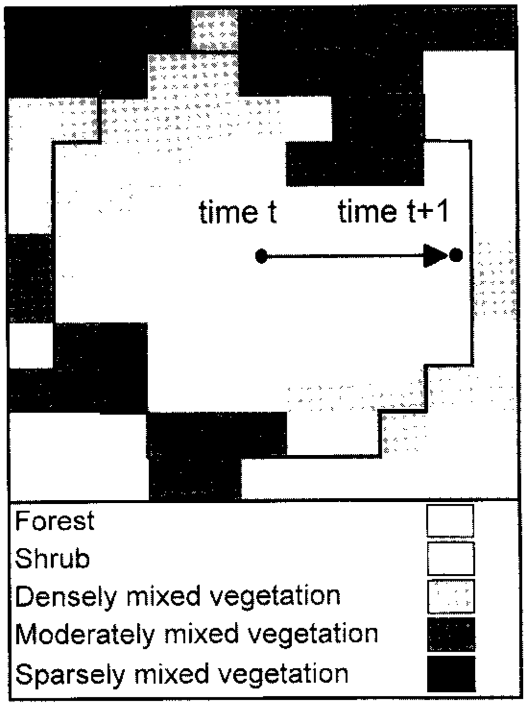

Figure 2. A single coyote movement represented by a straight line connecting relocations taken 1-hour apart. Available habitat during this movement was based on the composition of habitat inside a circle (actually a polygon on raster based maps), outlined here in black, with radius equal to movement distance. Used habitat was based on the composition of habitat intersected by the line connecting points t and t + 1. Each square represents a pixel 28.5 m on a side.

of habitat. Habitat types in my study area tended to occur in patches larger than a single pixel (i.e., pixel types were clumped in their distribution, unpubl. data). Thus to efficiently generate a proportion of *available* habitat that was different (and therefore comparable to *used* habitat) in its composition from a *used* proportion, the movement had to be large relative to the scale of clumping. Second, I had little guidance on appropriate time intervals from published literature since no one to my knowledge had looked at coyote movements as a function of habitat preference in this way and there were no studies of coyote movements in urban habitats to guide me. Finally, I chose the relocation time interval *a priori*. I was conservative in my use of statistics and in making conclusions because I *did* simplify coyote movements. I used a P value of 0.05. I chose not to weight compositional analysis by number of radio locations because it would have made it easier to find pattern (i.e., reject the null hypothesis that habitat use was random).

I obtained radio locations using a Yagi antenna with a 95% error arc ($\theta_{95} \pm 2$ SD, Springer 1979) of 16.2° (n = 10). I took most (>90%) bearings from locations within 400 m of the animals. At distances of 400 m and with bearings at 90° to each other, the 95% error polygon was approximately 13,071 m^2 (an area represented by 4 x 4 pixels). To minimize actual bearing error, I took three bearings per animal whenever possible and in most cases was able to get very near the animal because of the extent of roads in the urban areas. I found no evidence of bias in my telemetry equipment. Since my study was a comparative one (i.e., use vs. availability) random measurement error should make it more difficult to detect significant differences among use of habitats; that is, more difficult to reject the null hypothesis that use of habitat was proportional to availability.

Geographical Analysis Telemetry Locations

I plotted radio locations of coyotes on 1:24,000-scale topographic maps and assigned Universal Transverse Mercator (UTM) coordinates for each. These coordinates were entered into a database read by Geographical Resources Analysis Support System (GRASS 4.1, U.S. Army Corp. Eng., Construction Eng. Res. Lab. Champaign, Illinois). A GRASS procedure overlays each set of coordinates on an existing geo-referenced base map.

I conducted analyses of telemetry locations in GRASS using a habitat database from a 1985 LANDSAT image of King County. Personnel at the University of Washington Remote Sensing Laboratory used aerial photographs and field verification to classify each pixel, which corresponded to a square parcel 28.5 m on a side, into 1 of 13 different habitats. Overall accuracy (Story and Congalton 1986) of the classified map was 88% (King Co. Open Space Program 1987, King County, Wash., unpubl. data). For this study, I removed freshwater habitat and grouped together other similar types so the study area was represented with 5 habitats (Table 1): (1) Forest—areas dominated (>70%) by trees >6 m in height, >50%

TABLE 1. Proportions of habitat types composing the study area, 100% adaptive kernel home ranges (AKHR), and available habitat during routine movements of coyotes in the greater Seattle metropolitan area, 1989–90. Available habitat for a coyote was based on the composition of habitat inside circles with radius equal to movement distance of that coyote.

		AKHR						Movement Distance (m)		Available Habitat During Routine Movements				
Animal No.	#[a]	Forest	Shrub	Densely Mixed Vegetation	Moderately Mixed Vegetation	Sparsely Mixed Vegetation	#[b]	Mean	(SE)	Forest	Shrub	Densely Mixed Vegetation	Moderately Mixed Vegetation	Sparsely Mixed Vegetation
1	42	0.316	0.219	0.117	0.248	0.100	35	386.2	(54.3)	0.442	0.206	0.080	0.193	0.079
2	72	0.089	0.163	0.149	0.367	0.232	60	402.9	(75.5)	0.129	0.189	0.173	0.313	0.196
3	162	0.065	0.142	0.132	0.390	0.271	135	334.6	(61.9)	0.104	0.176	0.141	0.366	0.213
4	306	0.306	0.212	0.092	0.276	0.113	255	302.0	(53.0)	0.446	0.229	0.057	0.199	0.069
5	144	0.137	0.193	0.153	0.401	0.115	120	124.4	(20.2)	0.202	0.199	0.155	0.322	0.122
6	72	0.115	0.105	0.107	0.407	0.267	60	200.2	(29.3)	0.244	0.221	0.126	0.305	0.104
Habitat composition of the study area														
		0.093	0.124	0.120	0.399	0.264								

[a] Sample size of radio locations on which habitat compositions for AKHRs and the study area were based.
[b] Sample size of movements on which composition of available habitat during routine movements was based.

must be native tree species; (2) Shrub—areas dominated (>50% cover) by any combination of uncut grass, shrubs, or trees 1 - 6 m in height; (3) Densely mixed vegetation—areas dominated (>70%) by any combination of vegetation including shrub and forest, but contained ≤50% shrub cover or 70% tree cover, and ≥50% of the total plant cover was composed of nonnative species. This habitat was characterized by relatively high income housing developments with densities of 1-4 single family houses/ha; (4) Moderately mixed vegetation—areas in which any combination of vegetation types composed 30-70% of total ground cover, ≥50% of the total plant cover consisted of nonnative species, and ≤70% of the total ground cover could be covered by structures and impervious surfaces. This habitat characterized most residential development in King County with densities of 5-12 single family houses/ha; (5) Sparsely mixed vegetation—areas in which any combination of vegetation types composed <30% of the ground area. This habitat characterized most industrial development in King County including downtown metropolitan areas. There were few, if any, single family houses in this habitat.

Compositional Analysis

I used compositional analysis (Aebischer et al. 1993) to compare habitat selection at two spatial scales, i) home ranges versus study area, and ii) discrete areas of use, described either by coyote movement data or telemetry points, versus home ranges. Compositional analysis eliminates many of the common problems associated with habitat selection studies and uses the individual animal rather than a single telemetry location as the experimental unit (Aebischer et al. 1993, Aebischer and Robertson 1994). I used randomization tests provided in MacComp 0.90 (J. P. Carroll, The Game Conservancy, Fordingbridge, Hampshire SP6 1EF United Kingdom) to determine significance levels of Wilk's lambda (L) and t values used in the ranking matrices (Aebischer et al. 1993).

I defined the study area as the smallest area that included all coyote locations. Like many study areas, my study area was somewhat arbitrary because it included areas which were not trapped and were outside study animal home ranges. Using all radio locations for each animal, I calculated 100% adaptive kernel home range estimates (AKHR) (CALHOME, U.S. For. Ser. Pac. Southwest Res. Sta., Albany, CA) for each coyote. Sequential telemetry locations (as described above) were probably autocorrelated and may underestimate true home range size (Swihart and Slade 1985, but see Gese et al. 1990 and Reynolds and Laundré 1990). However, I was interested in delineating a boundary in which I could estimate habitat availability rather than home range size (Quinn 1995). Sequential locations as described above were appropriate for compositional analysis since tracking sessions were distributed in a relatively uniform manner throughout the sampling period (Aebischer et al. 1993:321).

The use of compositional analysis typically assumes equal sampling effort (same number of radio-locations) among animals. One way to account for the effect of unequal sampling effort among animals is to weight each animal's habitat composition by the number of radio-locations for that animal. Although weighting ensures that all animals contribute equally to the test of nonrandom habitat use, weighting might give too much emphasis to frequently observed animals. I chose not to weight samples by the number of radio locations, which resulted in a more conservative test (i.e., more difficult to reject the null hypothesis that habitat use was random (N.J. Aebischer, pers. comm.).

I calculated two estimates of habitat use based on movements: available habitat during movements, and used habitat during movements. For each movement, I defined available habitat as the composition of habitat inside a circle (actually a polygon on raster based maps) whose center was the location of the coyote at time t and whose radius was the movement distance from t to t + 1 (Figure 2). Habitat selection at this scale was akin to asking if coyotes moved in such a way as to remain in proximity to particular habitats types. I defined used habitat as the composition of habitat intersected by the straight line movement (Figure 2).

To estimate movement data habitat composition for a coyote, I summed the number of pixels of each habitat type across all movements (available or used habitat) by that individual and divided by the total number of pixels. An annual estimate was the only time frame for which I could analyze movement data since I did not have enough animals each season (a minimum of 6 is required) to test for seasonal effects (Aebischer et al. 1993). However, before pooling movement data, I determined that there was no difference (L = 0.708,

$P = 0.919$) between habitat available at night and habitat available during the day and no difference ($L = 0.798$, $P = 0.9630$) between habitat used at night and habitat used during the day.

Step-wise Regression of Movement Data

I used results from compositional analysis to quantitatively rank habitat quality from 1 to 5 where 1 is most preferred (Forest, Shrub, Densely mixed vegetation, Moderately mixed vegetation, and Sparsely mixed vegetation, respectively; see Table 2 for tests of significance among habitat types). I used stepwise multiple regression to examine the relationship between movement distance and quality of habitat in which the movement began (initial habitat), habitat in which the movement ended (final habitat), habitat gradient (initial - final habitat), and light conditions (night vs. day). The regression was designed to answer the question: are coyotes more likely to move long distances when they were in less preferred habitats. I initially used three different methods of calculating habitat quality: 1) the value of the single pixel in which an animal was located; 2) the sum of values for the nine pixel group (pixel in which the animal was located plus the eight surrounding pixels), and the mode of the nine pixel group. The idea behind using the sum and mode of a nine pixel group is that an animal may be responding to the "value" of habitat at larger scales than a single pixel. In other words, 9 pixels (3 x 3) of forest cover might be more preferred (affect movement distance more) than 9 pixels consisting of 5 forest and 4 moderately mixed vegetation. However, I excluded the 9 pixel sum and mode from further analysis because these measures were correlated ($r > 0.7$) with their single cell analogues (i.e., pixel types tended to be clumped in their distribution). I used a stepwise multiple regression on the pooled data set (all coyotes combined). I pooled movement data of all individuals based on results from compositional analysis, which indicated that habitat selection occurred at the level of my sample population.

The stepwise model fitting program used an alpha = 0.15 (F-test) to enter and remove predictors from the regression equation (Wilkinson 1992). I natural log-transformed the dependent variable [ln(movement distance +1)] to reduce the number of outliers, improve normality, linearity, and homoscedsticity of residuals (Sokal and Rohlf 1981). I removed 11 outliers after examining Studentized residuals resulting in a sample size of $n = 659$. Although some outliers are expected with a large data set such as this, all outliers I removed underestimated movement distance and skewed the distribution of residuals.

TABLE 2. Compositional analysis results for models comparing availability in the 100% adaptive kernel home range (AKHR) with 3 measures of habitat use within the home range: available habitat during movements, used habitat during movements, and habitat use based on telemetry points. Available habitat for a coyote was based on the composition of habitat inside circles with radius equal to movement distance for that coyote. Used habitat was based on the composition of habitat described by lines connecting consecutive relocations of a coyote at 1-hour intervals. Habitat types (Forest = FOR., Shrub = SHR, Densely mixed vegetation = DMV, Moderately mixed vegetation = MMV, and Sparsely mixed vegetation = SMV) are ranked in order of preference from left to right and are underlined when not different ($P > 0.05$) from each other.

Model Tested	P Value[a]	Individual Contrasts				
AKHR vs. Available Habitat	0.0360	FOR	SHR	DMV	MMV	SMV
AKHR vs. Used Habitat	0.0001	FOR	SHR	DMV	MMV	SMV
AKHR vs. Telemetry Points	0.0541	FOR	SHR	DMV	MMV	SMV

[a] P value is the probability that use of habitats was equal to availability of habitats for that model.

Results

I analyzed approximately 1 season of telemetry data (72 locations) from each of 3 coyotes, 2 seasons from each of 2 coyotes, and 4 seasons from 1 animal representing 11 coyote-seasons; 3 each from breeding, gestation, and pup-rearing seasons, and 2 from dispersal season. This represented 798 locations and 665 1-hour movements (Table 1). Animals for which I had <4 seasons of data either dispersed from the study area or died.

Compositional analysis revealed that coyotes established their home ranges at random ($L = 0.413$, $P = 0.631$) within the study area, which was composed of 9.3% Forest, 12.4% Shrub, 12.0% Densely mixed vegetation, 39.9% Moderately mixed vegetation, and 26.4% Sparsely mixed vegetation (Table 1). There was no difference ($L = 0.099$, $P = 0.205$) between available habitat and used habitat during movements. However, available habitat and used habitat during movements were different from expected based on the composition of home ranges ($L = 0.0340$, $P = 0.036$, $L = 0.0567$, $P < 0.0001$, respectively). Coyotes moved in such a way that available habitat and used habitat contained more Forest, Shrub, and Densely mixed vegetation and less Moderately and Sparsely mixed vegetation than the home range as a whole (Table 2). Habitat use based on telemetry points was not different from expected based on composition of home ranges ($L = 0.0420$, $P = 0.0541$; Table 2).

Of the 644 moves, 253 (39%) originated in Forest, 149 (23%) originated in Shrub, 121 (19 %) originated in Moderately mixed vegetation, 80 (12%) originated in Densely mixed vegetation, and 41 (6%) originated in Sparsely mixed vegetation. Step-wise multiple regression revealed that lighting conditions ($F = 7.647$, $P = 0.006$), and the interaction of lighting conditions and initial habitat type ($F = 8.139$, $P = 0.004$) were significant but weak predictors (multiple $R^2 = 0.137$) of movement length. Night movements were longer than day movements and movement distance tended to increase at night as initial habitat quality decreased (Figure 3). During the day, however, movement distance was relatively unrelated to initial habitat quality.

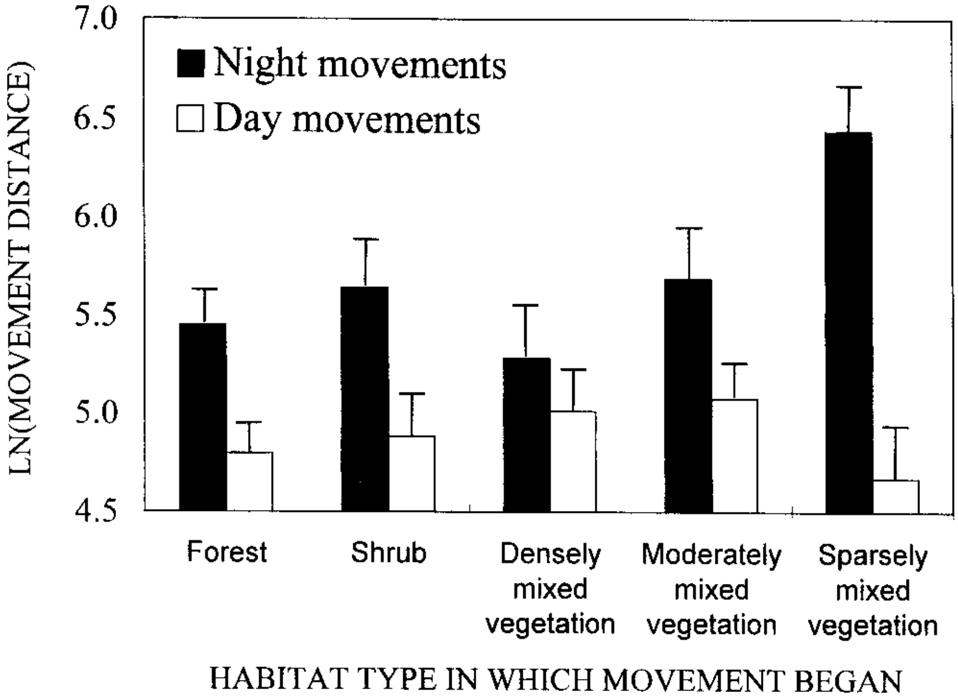

Figure 3. Mean movement distance (natural log transformed) and standard error in relation to lighting conditions (light vs. dark) and habitat type in which the movement began for coyotes in the greater Seattle metropolitan area, King County, Washington, 1989-90. Movements were represented by straight lines connecting consecutive radiolocations taken at 1-hour intervals.

Discussion

Analysis of movement data suggested that coyotes preferred relatively undisturbed habitats in urban environments of Washington State despite the fact that the amount of those habitats types (Forest and Shrub) was quite variable among home ranges and in some cases made up a small proportion of the home range (Table 1). Coyote selection for particular habitat was apparent only at the level of habitat use within the home range rather than at the level of the home range within the study area, although the failure to detect home range level habitat preference may have been an artifact of my study area description. Analysis of available habitat during movements, used habitat during movements, and to a lessor degree, habitat associated with telemetry points suggested that coyotes tended to prefer, in order of preference Forest, Shrub, Densely mixed vegetation, Moderately mixed vegetation, and Sparsely mixed vegetation (i.e., least disturbed to most disturbed). This was consistent with a previous habitat use study Quinn (1995) conducted on a temporally independent subset of the same telemetry data. Forest and Shrub probably provided the best hiding cover in urban western Washington. In addition, Shrub habitat which was typically found in transition areas between forest and more urbanized habitats may represent important foraging areas for coyotes in urban environments (Quinn 1997). Atkinson and Shackleton (1991) showed that the diet of coyotes near Vancouver, Canada, was dominated by 1 vole species (*Microtus townsendii*) found predominantly in grasslands. In this study grasslands were included in Shrub habitat.

While analysis of independent telemetry points revealed a similar but less conclusive pattern of habitat preference as movement data (also see Quinn 1995), analyzing movement data may expand the types of inferences that can be made about coyote behavior. For example data from both studies suggested that coyotes prefer relatively undisturbed habitats but movement data also suggested that coyotes remain in close proximity (within 1 hour travel time) of preferred habitat types, such as Forest and Shrub, during routine movements. Maintaining a close proximity to preferred habitats was not simply a function of home range habitat patterns since composition based on available habitat during movements was different from the composition of home ranges as a whole.

Nonrandom habitat use during movements may have been driven more by the avoidance of, than the selection for, particular habitat types. For example, Sparsely mixed vegetation had the strongest effect of all habitat types on coyote movement distance. Coyotes beginning their moves in Sparsely mixed vegetation traveled relatively long distances at night but tended to restrict movement length during the day, presumably to avoid contact with humans. In addition, few movements originated in Sparsely mixed vegetation despite the fact that this habitat typically made up a large percentage (≥10%) of coyote home ranges. Sparsely mixed vegetation, which may facilitate coyote travel at night became relatively unusable during the day. Sparsely mixed vegetation habitat is characterized by dense residential housing developments, major metropolitan areas, or industrial areas.

Heavily forested areas with low housing density provided the best daytime cover. Day movements were short possibly because they minimized the chance of being observed and/or because the best hiding habitat often occurred in small patches which limited the distance coyotes could move unobserved. Despite the fact that night movements were longer and less constrained by habitat type than day movements, urban coyotes still preferred relatively vegetated habitats at night.

Coyotes readily exploit human-derived foods (MacCracken 1982, Quinn 1997) in urban areas, which suggests that coyotes may benefit from some level of habitat disturbance even if it means limiting their movements to areas in or near undisturbed habitats. Coyotes in western Washington preferred portions of their home ranges that most resembled undisturbed habitats but persisted (or established home ranges) in urban areas with <25 % combined Forest and Shrub habitat. Thus, given the great variability in habitat compositions among coyote home ranges and the way coyotes structure their movements to stay close to hiding cover, the suitability of urban environments for coyotes may be more a function of the distribution rather than the overall quantity of preferred habitats.

I attempted to determine a general pattern of coyote habitat preference using a simple characterization of routine movements. Simplifying assumptions about animal movements will ultimately limit the usefulness of habitat preference studies because animals tend to move at different rates of speed depending on behavior (Laundré and Keller 1981). Ideally movement data could be analyzed at multiple temporal and spatial scales, which would allow researchers to address questions about habitat preference during specific behaviors (e.g., foraging) and how different relocation time intervals affect conclusions about habitat use. Better resolution of habitat base maps and advances in technology such as the use of satellite telemetry will greatly improve our ability to examine how animal behavior is structured by the distribution and types of habitat.

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