

Home Range Use of Coyotes: Revisited

Abstract

The sagebrush-steppe is a seemingly homogeneous community in southeastern Idaho, nevertheless coyotes in this community do not use their home ranges uniformly. Also, they display two different movements: back-and-forth (B) and ranging (C). We used a GIS analysis to test if coyotes were selecting specific habitat characteristics in this community and if there was a relationship between habitats selected and B and C type movements. Our results show that coyotes exhibit habitat selection within their home range with sagebrush on and off lava as the preferred habitats. They also selected primarily sagebrush-steppe on lava habitat for B movements and sagebrush off lava habitat for C movements. During their 24 hr travels, males and females used different habitat combinations for both B and C movements. Males primarily used the sagebrush on and off lava habitats while females commonly used a wider range of habitat types. There were significant differences in habitat composition of areas coyotes used daily relative to season. Coyotes in general used a greater diversity of habitat types during the pair formation and pup rearing but concentrated their activity in the sagebrush-steppe on lava habitat during gestation. We suggest that coyotes used differing behaviors in different habitat types to meet their daily/seasonal food needs.

Introduction

Coyotes are medium sized canids that occupy a variety of habitats in much of North America. Because of their ubiquitous distribution and frequent conflicts with human activities, there have been numerous studies of their ecology and behavior. Various investigators have studied habitat selection and have amply demonstrated that coyotes prefer certain habitat types and actively avoid others (Ozoga and Harger 1966, Gipson and Sealander 1972, Berg and Chesness 1978, Andelt and Gipson 1979, Litvaitis and Shaw 1980, Roy and Dorrance 1985, Gese et al. 1988, Holzman et al. 1992, Hernández et al. 1993, Murry et al. 1994). Additionally, some have reported differences in habitat use among seasons (Person and Hirth 1991).

In addition to demonstrating habitat selection by coyotes, some investigators have implied coyotes will select habitats for different behaviors such as for resting (Andelt and Gipson 1979) or for hunting (Chesness and Bremicker 1974, Murry et al. 1994, Oehler and Litvaitis 1995). Others have even shown that hunting success varies among habitat types (Murry et al. 1994, Gese et al. 1995), providing a possible rationale for preferred use. However, the main objective of these studies was not to test the hypothesis that coyotes were selecting different habitats for different behaviors.

Coyotes in southeastern Idaho use two distinct movement types within the 24-hr cycle (Laundré and Keller 1981). Type B movements are characterized by relatively small distances (<0.25 km) between relocations and produced a back and forth or zig zag pattern. Type C movements were characterized by longer distances between relocations which produced a much more elongated pattern. They also found home ranges consisted of areas of high and low use reflecting different combinations of frequency of use of these movement types. Additionally, coyotes use different proportions of types B and C movements between the sexes and through the year. Laundré and Keller (1981) proposed that these two movement types possibly represented different hunting strategies and that dissimilarities in their use represented differences/changes in the needs of males and females over the reproductive cycle, for instance, more territorial activity by males during pair formation (Camenzind 1978). Finally, they hypothesized that the differing spatial and temporal occurrence of the two behaviors corresponded to selection of habitat based on vegetational and structural differences in areas used for each strategy.

Laundré and Wilkosz (1991) attempted to test the hypothesis that areas used for different behaviors by coyotes were related to habitat composition by measuring various habitat characteristics of areas used by coyotes. They measured percent cover of each perennial plant species, litter, rock, bare ground, and dead sagebrush and

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found a weak association between types of behaviors and some habitat characteristics. However, the sample consisted of only four animals (two males and two females). They concluded a larger sample size would be necessary to test the hypothesis that coyotes selected certain habitat types for specific behaviors within the sage-steppe environment.

With the advent of Geographical Information System (GIS) capabilities, such a larger scale analysis is now possible. A detailed (30 m x 30 m pixels) GIS habitat map based on satellite images from 1987 and 1989 (Anderson et al. 1996) is now available for the area. Dominant community structure (shrubs-grasslands) does not change significantly over time (Anderson and Holte 1981). Thus, the overall habitat structure of the area would not have changed significantly in the 10 yr between collection of the telemetry data (1977-78) and the construction of the habitat map. Consequently, we have the opportunity to use this map with the original telemetry locations of coyotes, to test the hypothesis that different movements, and thus patterns of habitat use by coyotes, are related to different habitats.

We tested five predictions: 1) habitat characteristics of the home range area (the area coyotes select to live) will differ from the overall surrounding area (within 300 m around and including the home range area); 2) within the home range, areas of type B movement differ in habitat type compared to areas of type C movement; 3) the habitat types coyotes use for types B and C movements during their 24-hr travels differ; 4) the sexes use habitat differently for the two movement types; and 5) because coyotes exhibit a seasonal difference in the type of movements they use, there will be seasonal difference in overall daily habitat use.

To test these predictions and the hypothesis that coyotes are selecting different habitat types for different types of movements, we conducted a GIS analysis of habitat types relative to the different use types defined above. Results of our analysis should help determine if coyotes are selecting habitats based on their potential use for specific behaviors and further our understanding of the driving forces behind habitat selection.

Methods

The original telemetry study was on the Idaho National Engineering and Environmental Labo-

ratory (INEEL), located - 55 km north of Pocatello, Idaho. The vegetation is typical of a northern cool desert with big sagebrush (*Artemisia tridentata*)-grass communities (Anderson and Holte 1981, Anderson et al. 1996). The habitat map we used was based on two satellite images from 8 May 1987 and 17 August 1989. Pixel size was 30 x 30 m. The map was extensively ground checked and corrected in 1990 (Anderson et al. 1996). We used nine vegetation classifications, as defined by Anderson et al. (1996), for our analysis (Table 1).

The telemetry data for this analysis came from the study of Laundré and Keller (1981) conducted in 1976-79. The data consisted of 69 24-hr monitoring blocks from 20 animals (9 females and 11 males). Each 24-hr monitoring block consisted of sequential relocations taken every 15 min. In the original study, the sample animals (n =20) were a random subset of over 80 collared animals and were well distributed around the INEEL. Except for one mated pair, their home range areas did not overlap. Thus we considered the samples to be statistically valid for the analyses we used to test the predictions. The location error for the system of this study was ± 140 m. To incorporate this error, we included a 300 m buffer (150 x 150m) around telemetry locations and movement trajectories when we overlaid them on the habitat map.

We used similar preliminary map procedures to test if coyotes selected specific habitat types for their overall home range area (Prediction 1) and for different types of movement (B and C) within the home range area (Prediction 2). In both cases, we first defined home range areas of coyotes by the grid method (Laundré and Keller 1981) with 30 x 30 m grid cells. We estimated levels of use (time spent, distance traveled, and velocity) within each grid cell based on the 15-min sequential relocations over 24-hr monitoring blocks and then used these estimates to assign use types to each cell. Laundré and Keller (1981) demonstrated that a minimum of five 24 hr monitoring blocks were needed to adequately define a coyote's home range. Consequently, we only used data for five females and three males with five or more such time blocks (range: 5-10) for the home range area analyses.

We estimated habitat makeup of the home range areas by first constructing raster image files of the areas (30 x 30 m pixels) based on telemetry relocations. We georeferenced each of these image files to the habitat image based on the UTM coordinates of the original telemetry data. For each

TABLE 1. Vegetation classes from INEEL vegetation map used in the analyses of this study. Classification and descriptions are based on Anderson et al. (1996).

Habitat Class (ha)	Description
Basin Wildrye (BW) (735)	Near pure stands of Great Basin wildrye (<i>Leymus cinereus</i>)
Steppe Grassland (SG) (2,880)	Mixture of rhizomatous grasses (e.g. <i>Pascopyrum smithii</i>), bunchgrasses (e.g. <i>Oryzopsis hymenoides</i>), and shrub species (e.g. <i>Artemisia</i> spp.)
Grasslands (G) (11,065)	Areas dominated by rhizomatous grasses, bunchgrasses, or crested wheatgrass (<i>Agropyron desertorum</i>).
Sagebrush-Steppe off Lava (SS-off) (85,892)	Non volcanic soils with shrub-grass communities dominated by sagebrush.
Sagebrush- Steppe on Lava (SS-on) (90,366)	Areas of basaltic uplands with shrub-grass communities dominated by sagebrush.
Sagebrush - Winterfat (SW) (9,208)	Communities dominated by Wyoming big sagebrush and winterfat (<i>Krascheninnikovia lanata</i>).
Salt Desert Shrub (SD) (7,184)	Various salt desert shrubs primarily saltbrush (<i>Atriplex falcata</i>) and shadscale (<i>A. confertifolia</i>)
Sagebrush - Rabbitbrush (SR) (14,292)	Dominated by a mixture of sagebrush and green rabbitbrush (<i>Chrysothamnus viscidiflorus</i>).
Low Sagebrush/Rabbitbrush (SR-low) (1,531)	Areas of low growing (usually on lava) shrubs, primarily sagebrush (<i>Artemisia</i> spp.) and green rabbitbrush.

animal, we overlaid the home range image on the habitat image and made a section (windowed image) encompassing the home range area with a 300 m buffer to account for telemetry error (Figure 1a). The total windowed image was the area available to a coyote and the delineated home range was the area coyotes selected. We estimated the habitat makeup (total number of pixels per habitat type) of the total windowed image and, later, the home range area, with the histogram function of the IDRISI software. This function sums the number of pixels of each habitat type in the selected images.

Prediction 1

In testing prediction 1 (habitat characteristics within the home range will differ from surrounding areas), we tested to determine if the areas selected by coyotes for their home range differed in habitat from what was available in the whole area (home range included) within the 300 m buffer around the home range. We used a G-test (Sokal and Rohlf 1981) and calculated the number of expected pixels within the home range area from the proportion of each habitat type within the total image. We

used the number of pixels of each habitat type within the home range boundary as the observed values. The null hypothesis was that use of all habitats was in proportion to their availability. Because not all coyotes had the same habitat composition available (Table 2), we used the individual coyotes as the sample units and calculated separate G-tests for each individual.

Prediction 2

For Prediction 2 (within the home range, areas of type B and C movement will differ in habitat types), we used the same animals as in Prediction 1 (n = 8) and distinguished cells where animals used either types B or C movements with different cell values. We then separated each group of cell types from the rest of the home range cells with the use of boolean images (Eastman 1992). To construct a boolean image, we assigned 1.0 to all the desired cells (a given movement type) and 0.0 to all undesired cells. We overlaid these images (image 1 x image 2) on the original windowed image and obtained a final habitat image for a particular movement type (Figures 1b & 1c). In such an overlay, all desired cells retain their original

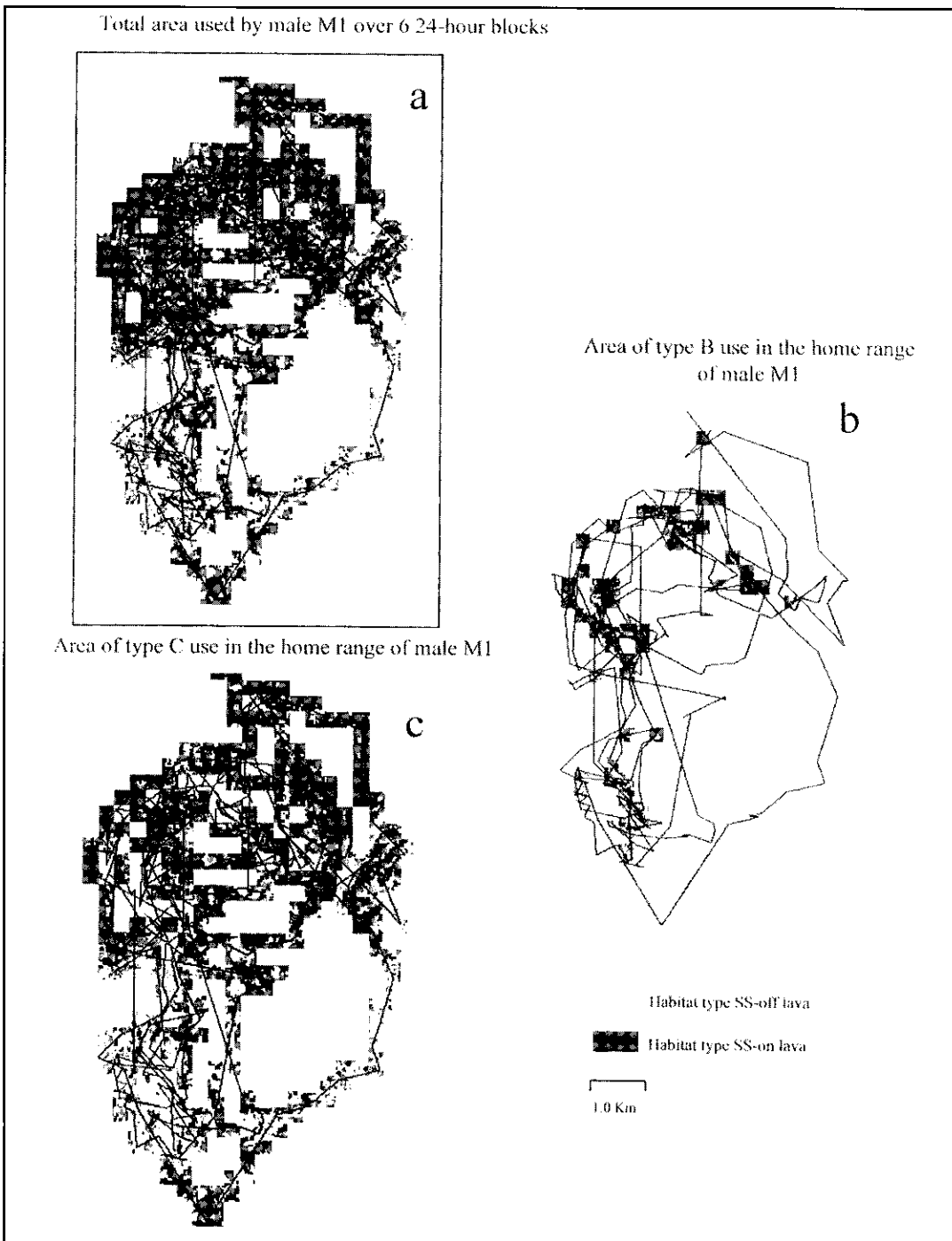


Figure 1. Demonstration of how habitat composition of the home range area (1a) and areas of type B (1b) and C (1c) use were determined. Once separated, the number of 30 x 30 m pixels of each habitat type were calculated with IDRISI software. The habitat of the total area encompassed by the border around 1a (including the defined home range) was used as the estimate of available habitat for testing the prediction of habitat selection for the home range area (Prediction # 1). For clarity, only the two most abundant habitat types are depicted here.

TABLE 2. Availability (percent of total in area) of the habitat types in the home range of each individual coyote used to test predictions 1 and 2; M = male, F = female. Habitat codes are explained in Table 1.

Habitat	Coyote ID number							
	M-1	M-2	M-3	F-1	F-2	F-3	F-4	F-5
BW	0.6	0.5	0.5	1.1	0.1	0.2	1.6	0.0
SG	0.5	3.0	1.0	3.1	0.8	0.0	2.9	0.5
G	1.8	7.5	5.8	8.3	6.5	2.2	11.2	2.0
SS-off	31.0	38.2	11.2	32.5	33.0	55.4	49.2	27.3
SS-on	60.8	36.4	80.1	34.5	37.7	30.3	7.5	1.2
SW	0.5	1.2	0.1	1.1	3.7	6.5	4.3	25.5
SD	0.1	1.8	0.0	2.3	6.3	1.5	3.2	16.5
SR	1.0	2.5	0.2	1.7	6.0	2.1	6.7	18.3
SR-low	1.8	1.1	0.5	1.3	3.5	0.1	0.0	0.0

value (multiplied by 1.0) and all undesired cells revert to a value of 0.0. Again, we obtained habitat composition of each movement type areas with the histogram function.

To compare if habitat composition differed between areas of type B and C movement, we first conducted a Principal Components Analysis (PCA) (Manly 1994) with the combined data of both movement types. We used a PCA because it effectively incorporated the contribution of multiple variables (via component loadings) of a given entity (i.e., area of specific movement type) and reduced them to one value (Z score) that described the entity. We then compared the Z scores for the appropriate treatments (type B and C movements) with univariate parametric statistical designs or their non parametric equivalents to determine if there were significant differences in habitat composition. The nine variables for the PCA were the percentages of each habitat type (Table 1) for each of the two movement types per animal. We used the resulting loadings for each variable to calculate Z_1 and Z_2 scores for the two types of areas of use for each animal. We compared the resulting Z_1 and Z_2 scores in a paired design with types B and C movement being the treatments and the different animals being the eight replicates. The null hypotheses were the mean differences in Z_1 or Z_2 scores between types B and C movement were not significantly different from zero.

Predictions 3, 4, and 5

To test Prediction 3 (habitats coyotes used for B and C movements differed during 24-hr travel) we used the telemetry data (15-min locations) for

each of the 69 individual 24-hr monitoring blocks we had for the 20 coyotes. For each block, we constructed a grid area similar to the home range grid area. However, in this case the grid cells defined an area used by the coyote during its 24-hr movements (daily range). As with the home range area, we assigned each cell a value for movement type (B or C) based on time spent, distance traveled, and velocity values for each. We then used the cells of these daily ranges to generate a raster image containing these use values. We georeferenced this daily range image to the habitat image and overlaid it on this image. We again separated the cells with different movement types with boolean images to obtain just those cells with either type B or type C movements. Finally, we calculated the habitat composition with the histogram function.

The result of the above analyses produced estimates of habitat composition for types B and C movements for each of the 69 24-hr monitoring blocks of the animals. We used the data for the two types of movements in a PCA that used the percentages of the different habitats as the variables. We used the loadings from this analysis to generate Z_1 and Z_2 scores for both type B and C areas for each 24-hr monitoring block. To avoid pseudoreplication for those animals for which we had more than one 24-hr monitoring block, we summed and averaged the replicate samples of animals, resulting in 20 individual paired component estimates (Z scores) of areas used for type B and C movements within a 24 hr block. Finally, we compared these paired estimates within a component (Z_1 or Z_2) with a paired-*t* design. The null hypotheses tested was the mean difference

in paired scores of areas used for types B and C movements for the first or second principal component was not significant from zero.

We tested Prediction 4 (the sexes should use habitat differently for the two movement types) with a two-way ANOVA design for Z_1 and Z_2 scores with movement type (B and C) and sex as the two levels. As we had tested differences in movement types with the more sensitive paired-t design (Prediction 3 above), here we used movement type primarily as a block (Sokal and Rohlf 1981) to test the main null hypotheses that the mean Z_1 nor Z_2 scores for these movement types did not differ significantly between males and females.

To test Prediction 5 (seasonal difference in daily habitat use), we used the 69 total daily range habitat images (i.e. total cells entered during a 24 hr block). As before, the percentages of each habitat from the daily ranges were the variables in a PCA with the 69 24-hr monitoring blocks being the replicates. We used the loadings for each variable to generate Z_1 and Z_2 scores for each block. We separated the Z_1 and Z_2 scores based on sex and season. We used the seasonal breakdown of Smith et al. (1981) with the following modifications: pair formation (Dec 1- Jan 31; 6 males, 4 females), gestation (Feb 1- Mar 15; 2 males, 3 females), and pup rearing (Mar 16- Aug 31; 7 males, 5 females) (Laundré and Keller 1984). We had no sample blocks for the dispersal season (Sept 1 - Nov 30). We used a two-way ANOVA design (sex x season) to test the null hypothesis that a mean component score (Z_1 or Z_2) did not differ significantly between sexes nor among seasons. Again, to avoid pseudoreplication, we calculated the means

of those animals that were represented by two or more 24-hr monitoring blocks within a given season. We used these mean values for these animals within their appropriate sex x season cell. Thus, each animal within a sex x season cell was only represented by one Z score.

We did all image processing and analyses with IDRISI32 software (Release 2, Clark Lab., George Perkins Marsh Institute, Clark University, Worcester, MA). For the principle component analyses we used Systat software (Version 5.02, Systat, Inc. Evanston IL) and for all statistical tests we used Sigmastat software (Version 2, Jandel Corp., San Rafael, CA). Means are \pm standard error and significance levels were $P \leq 0.05$.

Results

Regarding Prediction 1, habitats sagebrush-steppe off lava (SS-off) and sagebrush-steppe on lava (SS-on) were the most abundant available habitats for all animals, with the exception of coyote F5 where SS-off and sagebrush-winterfat (SW) predominated (Table 2). All eight coyotes selected for specific habitats ($P < 0.001$) (Table 3), thus supporting Prediction 1. The most selected habitat types were SS-off and SS-on (six of eight coyotes). Although one or both of these habitats were also abundant within the home ranges of the other two coyotes, M1 selected low sagebrush/rabbitbrush (SR-low) and F5 selected sagebrush-winterfat (SW).

Relative to the PCA analysis for prediction 2 (B and C movement areas within the home range areas correspond to different types of habitats), the first and second principal components explained

TABLE 3. G-test values to determine if coyotes (M = males, F = females) selected different kinds of habitat. Those values with asterisks were used significantly ($P \leq 0.05$) more (+) or less (-) than available. Habitat codes are explained in Table 1.

Habitat	Coyote ID number							
	M-1	M-2	M-3	F-1	F-2	F-3	F-4	F-5
BW	102.5	-24.6	-45.9	-117.0	1.8	24.6	-161.2	-0.6
SG	91.6	166.6	-21.9	-122.4	-64.9	-3.0	-151.3	-39.2
G	145.3	156.5	-508.5*	-427.8*	-41.3	-93.4	-780.4*	-41.1
SS-off	-469.9*	971.6*	-911.9*	784.2*	-1258.4*	200.3*	1953.9*	-1084.6*
SS-on	-154.8	-1048.9*	2524.5*	321.0	2216.9*	-69.5	675.5*	-31.5
SW	-3.4	-99.2	1.6	-56.2	-337.3	-239.6*	-430.9	1072.7*
SD	29.3	-40.8	-1.9	-187.3	-452.4	88.9	-267.2	234.6
SR	-9.4	126.7	-10.4	21.8	-182.2	179.4*	-681.6*	136.4
SR-low	407.8*	-29.9	46.6	3.0	824.9	4.2	0.8	0

61.8% of the total variance (Table 4). When we tested if the B and C movement areas correspond to different types of habitats, we used the Wilcoxon signed rank test to compare the Z_1 scores calculated from the PCA (Table 4). We found a significant difference ($P = 0.016$) between Z_1 scores for type B ($\bar{x} = 0.84 \pm 1.21$) and C ($\bar{x} = -0.84 \pm 1.24$) movement. We found no significant differences for the Z_2 scores. The value of a given Z_1 is a function of the component loading value and the magnitude of the standardized variable (percent use). As the loadings for each variable were the same for types B and C movements, the differences in Z_1 scores reflected habitats that had different percent use between the two movement types; habitats with the same percent use between movements contributed equally to their Z_1 scores. To identify which habitats might be contributing to the differences in Z_1 scores, we plotted the percent use of each habitat for types B and C movement (Figure 2) along with their respective component loadings. Since the component loading for habitat SS-on was large (0.807) and positive (Figure 2), the higher Z_1 scores for type B movements reflected the higher use of this habitat for type B movement compared to type C movement. Other differences in habitat use contributing to the differences in Z_1 scores were higher uses of SS-off (-0.25), SD (-0.81), and SR (-0.93) for type C movements (Figure 2). Habitat type

SW had a high negative loading (-0.81) but it was used equally for both movement types.

To test for differences in areas used for types B and C movements within the 24-hr monitoring blocks (Prediction 3), the PCA combined the data relative to types B and C movements within the 69 24-hr monitoring blocks. Percent variance explained by the first and second principal components was 66.3% (Table 4). When we analyzed Z_1 scores we found significantly higher ($P < 0.001$) scores in areas coyotes used for type C movement (0.82 ± 0.58) than for type B movement (0.03 ± 0.58) (Figure 3a). Again, there was no significant difference between the two movement types for Z_2 values. For the first component, the lower Z_1 scores for type B movement compared to type C (Figure 3a) primarily reflected higher use of the SS-on habitat which, in this case, had a high negative loading (Figure 3b) and lower use of the SS-off, G, and SR habitats relative to type C movements (Figure 3b).

When we compared habitat composition of areas used by males and females for types B and C movements during 24 hr (Prediction 4), we found significantly higher Z_1 scores for females than males ($P = 0.042$). Again, there was no significant difference for Z_2 scores. The difference between sexes for the Z_1 scores reflected higher scores for females compared to males for both type B and C movements (Figures 4a, 4c). For both

TABLE 4. Results of the various principal component analyses conducted to help test predictions #2-5 of this study. Prediction # 2 concerns the difference in habitat makeup of areas of types B and C use within the home range. Differences in habitat of areas used by coyotes in types B and C manner within a 24-hr monitoring block constitutes prediction #3. Prediction # 4 concerns differences in habitat use by males vs females for types B and C movements. Prediction # 5 states that there would be differences in habitat composition during daily use relative to season and sex of coyotes. The component loadings for the first and second principal component and the percent of the total variance explained are given. Component loadings for habitat Basin Wildrye (BW) are not presented because of its low occurrence and use. Habitat codes are explained in Table 1.

Prediction		Habitat Type							% Total Variance	
		SG	G	SS-off	SS-on	SW	SD	SR		Sr-low
2	Z_1	0.07	-0.12	-0.25	0.81	-0.81	-0.81	-0.93	0.44	33.5%
	Z_2	-0.61	-0.83	-0.92	0.54	0.42	0.33	0.33	0.41	28.3%
3 & 4	Z_1	0.26	0.32	0.51	-0.87	0.70	0.64	0.81	-0.53	37.9%
	Z_2	-0.68	-0.70	-0.62	0.29	0.56	0.51	0.46	0.28	28.4%
5	Z	0.24	0.16	0.40	-0.87	0.83	0.76	0.87	-0.54	41.2%
	Z_2	-0.69	-0.61	-0.72	0.39	0.50	0.51	0.37	0.42	29.2%

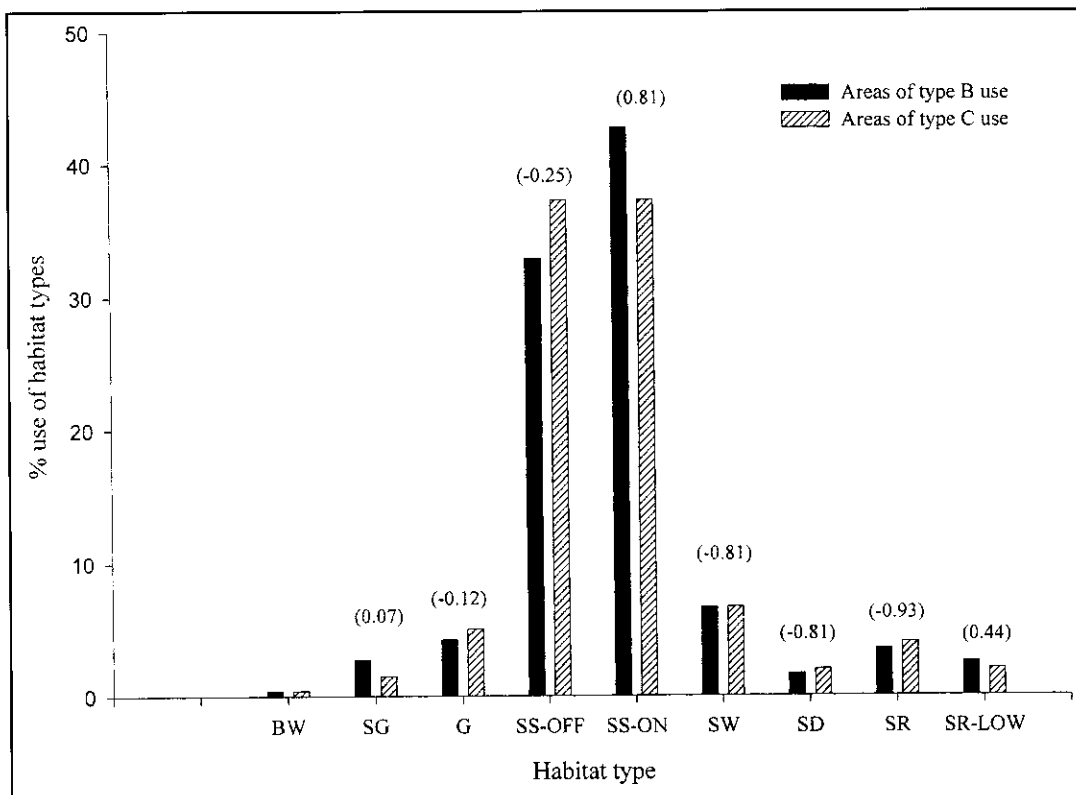


Figure 2. Habitat makeup (percent of total pixels) of areas within the home ranges coyotes used in either a type B or C manner. The component loadings resulting from the PCA are included for the eight most used habitats.

movements types, the higher Z_1 scores for females reflected lower use of SS-on and higher use of SS-off, SR, SD, and SW habitats when compared to males (Figures 4b, 4c). Basically, females used a wider range of habitat types than males for both types B and C movements.

Finally we also saw differences in habitat composition, as expressed by Z_1 , of areas coyotes used daily relative to season ($P = 0.04$) and sex ($P = 0.03$) (Prediction 5). Again, there was no significant difference for Z_2 scores. Relative to seasons, the mean Z_1 score for pair formation (1.5 ± 1.01) was significantly higher than for gestation (-2.16 ± 0.77) with pup rearing (0.14 ± 0.94) being intermediate between the other two (Figure 5a). An analysis of the component loadings for these PCAs and percentages of seasonal use (Figure 5) indicated lower Z_1 scores (Figure 5a) reflected a selection for habitat type SS-on and higher scores reflected higher uses of habitats G, SS-off, SW, and SR (Figure 5b). This means coyotes in gen-

eral were switching habitat use with a more diverse use of habitats during pair formation, a switch to higher uses of SS-on during gestation and then increasing again the use of other habitats during pup rearing.

Relative to the significant difference between sex, sample sizes were small but still indicated that the overall seasonal mean Z_1 score for females (1.6 ± 1.10) was significantly higher than for males (0.88 ± 0.50). The differences in Z_1 scores between sexes within seasons (Figures 6a, 6c, 6e) reflected a more diverse selection of habitats by females during pair formation (Figure 6b) and a higher use of SS-on (high negative loading) by males. During gestation (Figure 6d) both sexes concentrated their activity on SS-on and SS-off habitats but in different proportions; females used SS-off more whereas males used SS-on habitats more. During the pup rearing season, females again diversified their habitat use (Figure 6f) whereas males continued using the SS-on habitat.

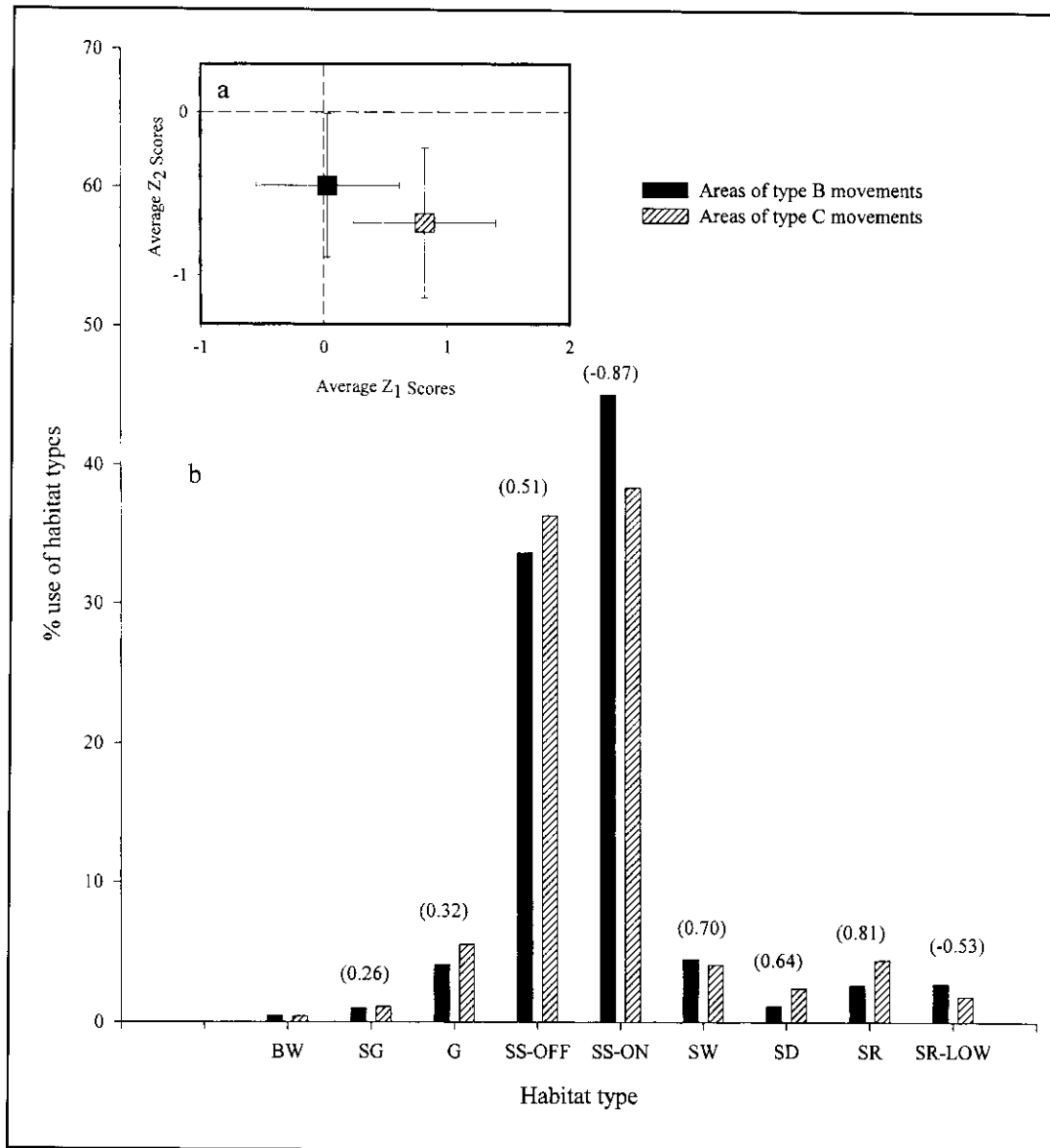


Figure 3. Plot of the Z_1 and Z_2 scores for areas of type B and C movements within the 24-hr time blocks (3a). Figure 3b is the habitat makeup (percent of total pixels) of areas within the 24-hr monitoring block where coyotes used type B and C movements. The component loadings resulting from the PCA are included for the eight most used habitats.

Discussion

Although the small sample size of our study (eight animals) may limit interpretation of our results, there is an indication that coyotes in our study area exhibited selection for specific habitats in defining their home range area. Additionally, we found the home range area likely has a basis in

the daily use of the back and forth and ranging movement types by coyotes (Figure 2). Because we defined coyote home range areas based on 24-hr monitoring blocks, this might be expected. However, areas would be designated for a given movement type only if its use predominated there. Thus, the use of the 24-hr monitoring blocks

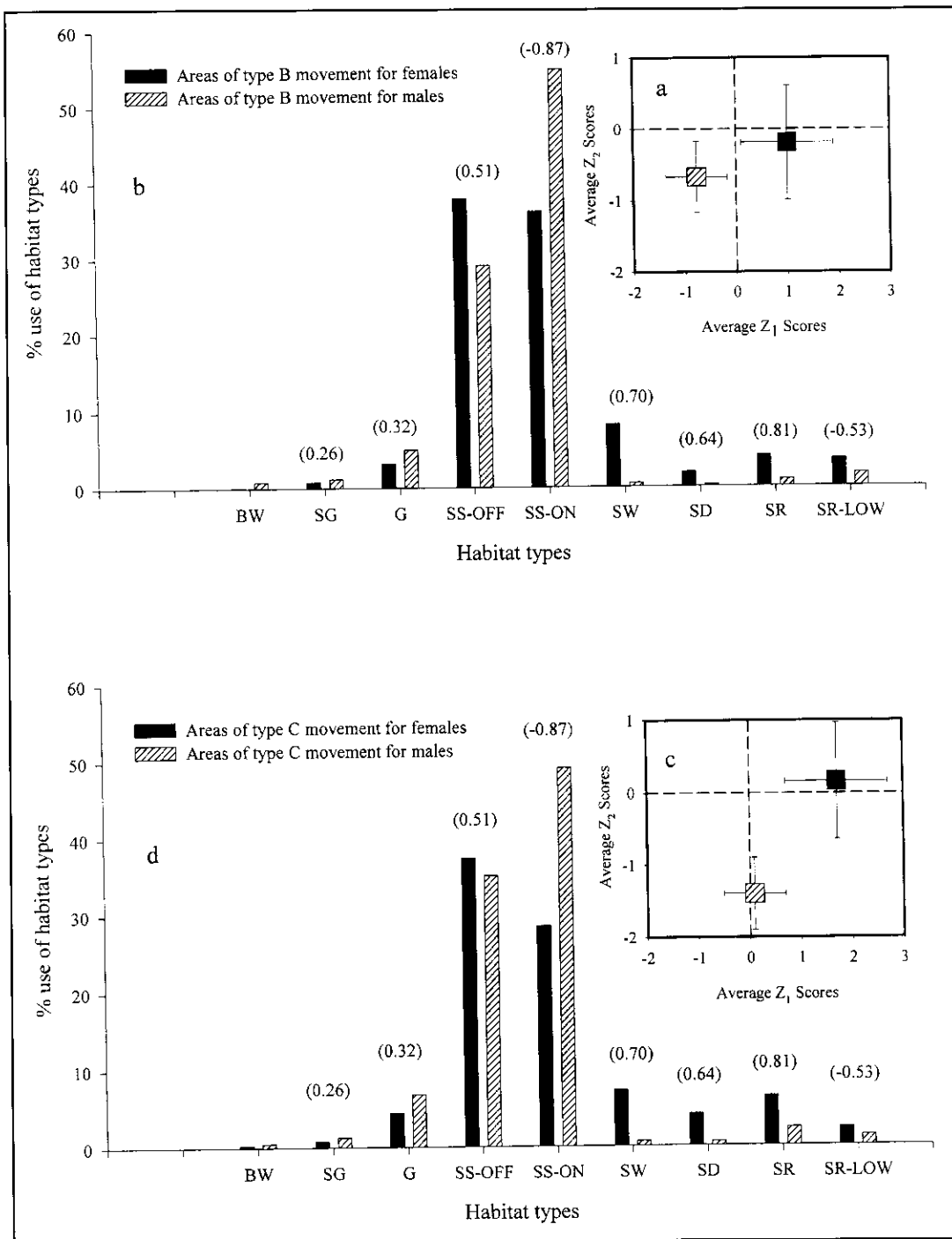


Figure 4. Plots of the Z_1 and Z_2 scores for female and male coyotes relative to types B (4a) and C (4c). Figures 4 b & d depict the habitat makeup (percent total pixels) of the areas female and male coyotes used for type B (4b) and C (4 d) movements within the 24-hr monitoring block. The component loadings resulting from the PCA are included for the eight most used habitats.

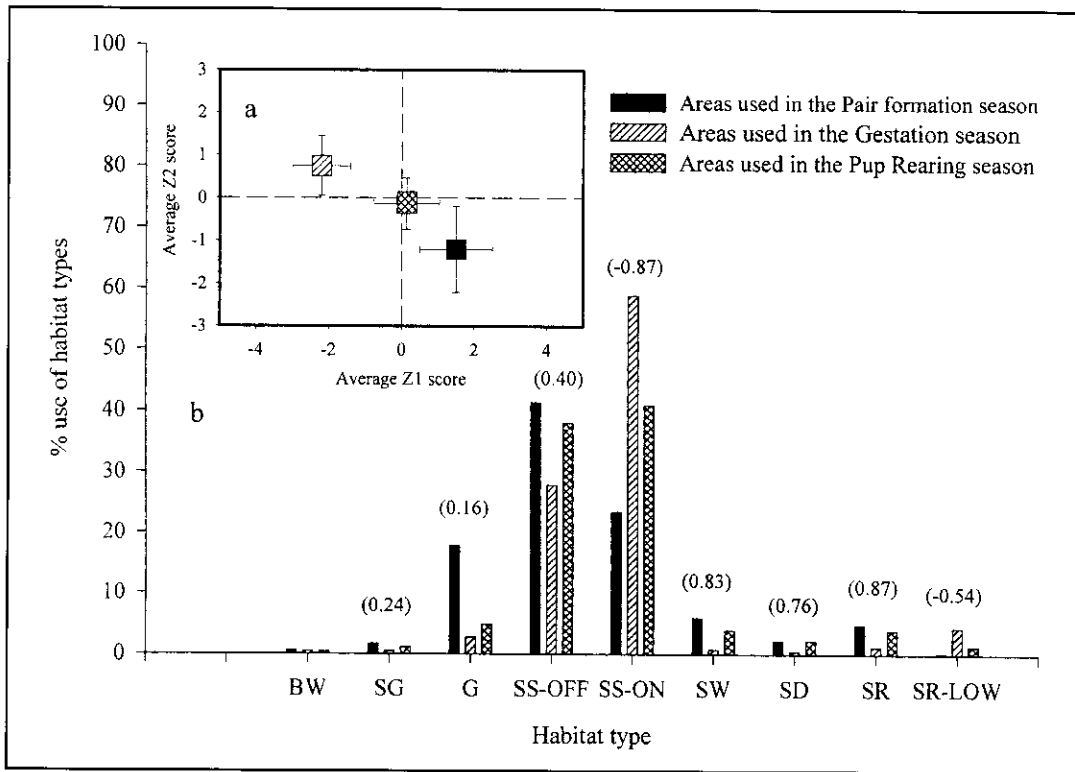


Figure 5. Plots of the Z_1 and Z_2 scores for areas used by coyotes for the three seasons: pair formation, gestation, and pup rearing (5a). Figure 5 b is of the habitat makeup (percent of total pixels) of areas coyotes used in 24-hours during the three seasons of pair formation, gestation, and pup rearing. The component loadings resulting from the PCA are included for the eight most used habitats.

delineates the home range area on a behavioral basis rather than merely a polygon containing a series of dots. The result is a home range area that represents how coyotes integrate their daily movements within the available habitats.

Our findings for Predictions 4 and 5 supported the hypothesis that habitat use should differ between sexes and among seasons and again, not only showed sexual differences and seasonal changes in habitat use, but also linked these differences to changes in behavior. For example, seasonal and sexual differences in the uses of types B and C movements (Laundré and Keller 1981) corresponded to shifts in the habitat composition of areas used for these movements (Figures 5,6). However, because of limited sample sizes in some sex x season categories, these results should be interpreted cautiously. Additional data in this area would help clarify these relationships.

The idea of habitat selection by coyotes is not new (Ozoga and Harger 1966, Gipson and Sealander 1972, Berg and Chesness 1978, Andelt and Gipson 1979, Litvaitis and Shaw 1980, Roy and Dorrance 1985, Gese et al. 1988, Holzman et al. 1992, Hernández et al. 1993, Murry et al. 1994). However, in most other studies, coyotes often selected among quite discrete habitats (wheat fields vs. pasture). Hernández et al. (1993) were some of the first to demonstrate that fine habitat characteristics (e.g. shrub density and topographic features), may influence coyote habitat use. Our results concur with those of Hernández et al. (1993) and we now have ample data that coyotes exhibit preferences in habitat use ranging from areas containing discrete vegetational patterns to those where habitats change in more subtle ways.

Given that coyotes do select habitat combinations based on their different use of these areas,

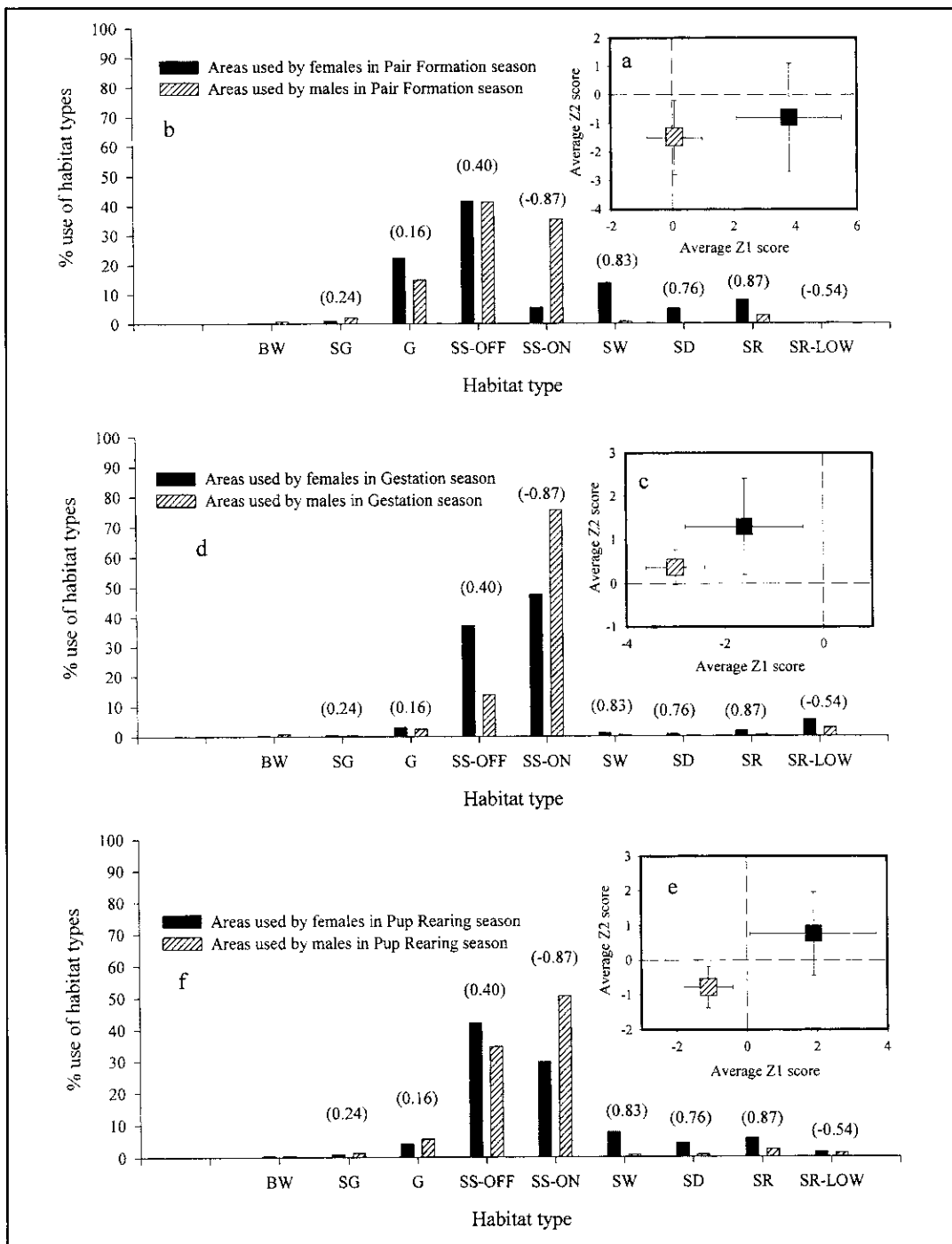


Figure 6. Plots of the Z_1 and Z_2 scores for males and females for each of the three seasons, pair formation (6a), gestation (6c) and pup rearing (6e). Figures 6 b, d, & f are of the habitat makeup (percent of total pixels) of areas female and male coyotes used in 24-hours during the pair formation, gestation, and pup rearing seasons. The component loadings resulting from the PCA are included for the eight most used habitat.

the questions still remains as to why? Optimal foraging theory predicts predators will make habitat use (patch) decisions based primarily on food availability and ease of capture (Brown et al. 1999). Hernández et al. (2002) have demonstrated that coyotes incorporate optimal foraging approaches in their diet selection. Also, others have demonstrated that prey in response to predation risk will alter their behavior and habitat use patterns (Laundré et al. 2001, Altendorf et al. 2001, Marín et al. 2003). Within this landscape of fear created by predation risk (Laundré et al. 2001), composition and densities of coyote prey will vary among habitats (Murry et al. 1994, Marín et al. 2003) and capture success can differ relative to habitat type (Murry et al. 1994, Gese et al. 1995). This produces an inverse landscape of opportunity for coyotes relative to prey capture. If the two movement types represent different hunting patterns then one hypothesis is that coyotes of this study exhibit differing hunting behaviors in various parts

of their home range because of different prey composition/density/catchability found there.

Further research needs to test the link between behavioral use of a habitat type and prey composition and how well optimal foraging theory might explain movement patterns and habitat selection by coyotes. If these models are supported by future research, we will then have a deeper understanding of the driving forces behind habitat preferences in coyotes. This increased understanding could help us in our effort to manage our coexistence with this ubiquitous predator, specifically in rangeland areas where conflicts are frequent.

Acknowledgements

The original data for this analysis were collected under a grant from the Office of Health and Environmental Research Division, U.S. Department of Energy to B.L. Keller. We again thank all those persons acknowledged in this original publication.

Literature Cited

- Altendorf, K. B., J. W. Laundré, C. A. López González, and J. S. Brown. 2001. Assessing effects of predation risk on foraging behavior of mule deer. *Journal of Mammalogy* 82:430-439.
- Andelt, W. F., and P. S. Gipson. 1979. Home range, activity, and daily movements of coyotes. *Journal of Wildlife Management* 43:944-951.
- Anderson, J. E., and K. E. Holte. 1981. Vegetation development over 25 years without grazing on sagebrush-dominated rangeland in southeastern Idaho. *Journal of Range Management* 34:25-29.
- Anderson, J. E., K. T. Ruppel, J. M. Glennon, K. E. Holte, and R. C. Rope. 1996. Plant communities, ethnobotany, and flora of the Idaho National Engineering Laboratory. Unpublished report ESRF-005 Environmental Science and Research Foundation, Idaho Falls, Idaho.
- Berg, W. E., and R. A. Chesness. 1978. Ecology of coyotes in northern Minnesota. Pages 229-247 *In* M. Bekoff (editor), *Coyotes: Biology, Behavior, and Management*. Academic Press, New York.
- Brown, J. S., J. W. Laundré, and M. Gurung. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy* 80: 385-399.
- Camenzind, F. J. 1978. Behavioral ecology of coyotes on the National Elk Refuge, Jackson, Wyoming. Pages 267-294 *In* M. Bekoff (editor), *Coyotes: Biology, Behavior and Management*. Academic Press, New York.
- Chesness, R. A., and T. P. Bremicker. 1974. Home range, territoriality and sociability of coyotes in northcentral Minnesota. Paper presented at 1974 Coyote Workshop, Denver, Colo. Minnesota Department of Natural Resources, Grand Rapids, Minnesota.
- Eastman, J. R. 1992. Idrisi. Technical reference. Version 4.0. Clark University, Worcester, Mass.
- Gese, E. M., O. J. Rongstad, and W. R. Mytton. 1988. Home range and habitat use of coyotes in southeastern Colorado. *Journal of Wildlife Management* 52:640-646.
- Gese, E. M., R. L. Ruff, and R. L. Crabtree. 1995. Intrinsic and extrinsic factors influencing coyote predation of small mammals in Yellowstone National Park. *Canadian Journal of Zoology* 74:784-797.
- Gipson, P. S., and J. A. Sealander. 1972. Home range and activity of the coyote (*Canis latrans frustror*) in Arkansas. Pages 82-95 *In* Proceedings of the 26th Annual Conference of Southeastern Association of Game and Fish Commissioners, Nashville, Tennessee.
- Hernández, L., M. Delibes, and E. Ezcurra. 1993. Activity pattern, home range, and habitat preference by coyotes (*Canis latrans*) in the Mapimi Biosphere Reserve of the Chihuahuan Desert, Mexico. *Doñana, Acta Vertebrata* 20:276-282.
- Hernández, L., R. R. Parmenter, J. W. Dewitt, D. C. Lightfoot, and J. W. Laundré. 2002. Coyote diets in the Chihuahuan Desert, more evidence for optimal foraging. *Journal of Arid Environments* 51:613-624.
- Holzman, S., M. J. Conroy, and J. Pickering. 1992. Home range, movements, and habitat use of coyotes in southcentral Georgia. *Journal of Wildlife Management* 56:139-146.
- Laundré, J. W., and B. L. Keller. 1981. Home-range use by coyotes in Idaho. *Animal Behaviour* 29:449-461.
- Laundré, J. W., and B. L. Keller. 1984. Home-range of coyotes: a critical review. *Journal of Wildlife Management* 48:127-139.
- Laundré, J. W., and R. J. Wilkosz. 1991. The use of cluster analysis to analyze habitat use by coyotes in an area

- of low vegetal heterogeneity. *Northwestern Naturalist* 72:12-20.
- Laundré, J. W., L. Hernández, and K. B. Altendorf. 2001. Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology* 79:1401-1409.
- Litvaitis, J. A., and J. H. Shaw. 1980. Coyote movement, habitat use, and food habits in southwestern Oklahoma. *Journal of Wildlife Management* 44:62-68.
- Manly, B. F. J. 1994. *Multivariate Statistical Methods: a Primer*. 2nd edition. Chapman and Hall, London, U.K.
- Marín, A. I., L. Hernández, and J. W. Laundré. 2003. Predation risk and food quantity in the selection of habitat by black-tailed jackrabbit (*Lepus californicus*): an optimal foraging approach. *Journal of Arid Environments* 55:101-110.
- Murry, D. L., S. Boutin, and M. O'Donoghue. 1994. Winter habitat selection by lynx and coyotes in relation to snowshoe hare abundance. *Canadian Journal of Zoology* 72:1444-1451.
- Oehler, J. D., and J. A. Litvaitis. 1995. The role of spatial scale in understanding responses of medium-sized carnivores to forest fragmentation. *Canadian Journal of Zoology* 74:2070-2079.
- Ozoga, J. J., and E. M. Harger. 1966. Winter activities and feeding habits of northern Michigan coyotes. *Journal of Wildlife Management* 30:809-379.
- Person, D. K., and D. H. Hirth. 1991. Home range and habitat use of coyotes in a farm region of Vermont. *Journal of Wildlife Management* 55:433-441.
- Roy, L. D., and M. J. Dorrance. 1985. Coyote movements, habitat use, and vulnerability in central Alberta. *Journal of Wildlife Management* 49:307-313.
- Smith, G. J., J. R. Cary, and O. J. Rongstad. 1981. Sampling strategies for radio-tracking coyotes. *Wildlife Society Bulletin* 9:88-93.
- Sokal, R. R., and F. J. Rohlf. 1981. *Biometry*. Freeman. San Francisco, California.

Received 13 August 2001

Accepted for publication 21 April 2003