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Comparison of Coyote Diets Between Two Areas of Jackson Hole, Wyoming

Abstract

Coyotes (Canis latrans) *have moved into urban and suburban areas across North America, presumably taking advantage of anthropogenic food sources. We compared diets between coyotes in an undeveloped and a suburban/agricultural area in Jackson Hole, Wyoming from July 1998 to August 1999. We analyzed 170 and 169 scats from the suburban/agricultural and the undeveloped area, respectively. Voles* (Microtus *spp.) were the predominant prey item in scats from both areas during all seasons. Scats collected in the suburban/agricultural area had a significantly higher percent occurrence of voles during all seasons and annually (49%) than the undeveloped area (24%). Coyotes from the undeveloped area consumed significantly more pocket gophers* (Thomomys talpoides) *in summer and more cervids in winter than coyotes from the developed area. Foods of human origin were rarely found in scats. We used Sherman live traps to assess relative availability of small mammals. More voles were captured in the suburban/agricultural area than in the undeveloped area. Deer mice* (Peromyscus maniculatus) *were most frequently captured mammals in both study areas, but they comprised <1 percent of the diet. This study confirms the generalist nature of the coyote with the exception that the coyotes consumed few deer mice, which appeared to be highly abundant in the area. Coyotes in the suburban/agricultural area took advantage of an abundant vole population that may have been elevated due to human disturbances.*

Key words: agriculture, *Canis latrans*, coyote, diet, prey, scat analysis, suburban development, Wyoming

Introduction

Recently, coyotes (*Canis latrans*) have moved into suburban and urban areas (MacCracken 1982, Atkinson and Shackelton 1991, McClure *et al.* 1995, Quinn 1997). They have been able to do this because they are dietary generalists, and because human-influenced or disturbed areas provide an abundant food source (Shargo 1988, Toweill and Anthony 1988). Most dietary studies of urban and suburban coyotes have found that these coyotes supplement their diets with foods that are related to human presence (e.g. MacCracken 1982, Atkinson and Shackelton 1991, McClure *et al.* 1995, Quinn 1997). However, few of these studies occurred in areas where dietary comparisons could be made between adjacent developed and undeveloped areas (McClure *et al.* 1995).

Local prey abundance is one of the major factors that regulates coyote abundance (Knowlton and Gese 1995). Developed areas may have an artificially enhanced food base as a result of domestic pets, pet food, garbage, and rodents associated with humans (Shargo 1988). Shargo (1988)

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explained the high coyote density he found in urban areas of Los Angeles as a result of plentiful food sources, which were a result of both human activities and a productive habitat. Increased food availability in urban and suburban settings may allow coyotes to successfully live in those areas at high densities, and thus may, in part, ultimately cause human/coyote conflicts. Because coyotes also rely on human related foods, they may approach human-inhabited areas closer than many people's comfort level warrants.

Coyotes in developed areas apparently can exploit resources offered by urban, suburban, and agricultural settings while minimizing risks associated with being in close proximity to people. Coyotes tend to exist at high densities and oocupy smaller home ranges in urban and suburban areas than they do in undeveloped areas (Shargo 1988, McClennen 2000, McClennen *et al.* 2000). When food is plentiful, coyote densities may increase (Atkinson and Shakelton 1991, Knowlton and Gese 1995).

Our objective was to compare diets of coyotes in developed and undeveloped areas of Jackson Hole, Wyoming. We predicted that coyotes in the developed area would use more human associated foods such as garbage, pets, and livestock. Additionally, we hypothesized that coyotes in the undeveloped area would consume more wild ungulates such as elk (*Cervus elaphus*), moose (*Alces alces*), bison (*Bison bison*), deer (*Odocoileus hemoinus, O. virginianus*), and pronghorn (*Antilocapra americana*).

Materials And Methods

Study Area

We designated two study areas in the valley of Jackson Hole (43° 40' latitude, 110° 43' longitude) in northwest Wyoming (Fig. 1). The undeveloped area (UNDA) encompassed southern Grand Teton National Park (GTNP), the National Elk Refuge (NER), and parts of Bridger-Teton National Forest (BTNF). This area has little human influence, and was relatively undisturbed. Housing density in areas that coyotes used ranged from 0 - 0.08 houses/ha. Kelly, Wyoming, with a human population of 200, one campground, and a few small private inholdings are located within the UNDA. Cattle grazing was permitted during limited times on specified allotments during summer in GTNP.

The suburban/agricultural study area (SAA) surrounded the towns of Jackson and Wilson, Wyoming. It was bordered by GTNP to the north, BTNF to the east and west, and the NER to the east. This area consisted of private land primarily devoted to agricultural, commercial, and residential uses. Cattle ranching was a major land use. Housing density in areas that coyotes used ranged from 0.03 - 0.99 houses/ha.

Jackson Hole is a high valley with elevations averaging 1880 m in the SAA and 2014 m in the UNDA. Summers are short and winters are long. Precipitation most often occurs in the form of snow from October to April. Mean annual precipitation (1961-1990) was 42 cm in the SAA area and 54 cm in the UNDA. Mean annual temperatures (1961-1990) ranged from -9 to 16 °C in the SAA area and -11 to 16 °C in the UNDA (High Plains Climate Center, Lincoln, NE).

Diet Analysis

We collected coyote scats approximately every six to eight weeks from July 1998 to August 1999 on transects along trails and dirt roads. Initially, we cleared scats from each transect to ensure that only scats deposited in a known time period were collected. Approximately 33 and 22 km of transects were walked in GTNP and the SAA, respectively. Transect lengths ranged from 1.4 - 3.0 km in the UNDA

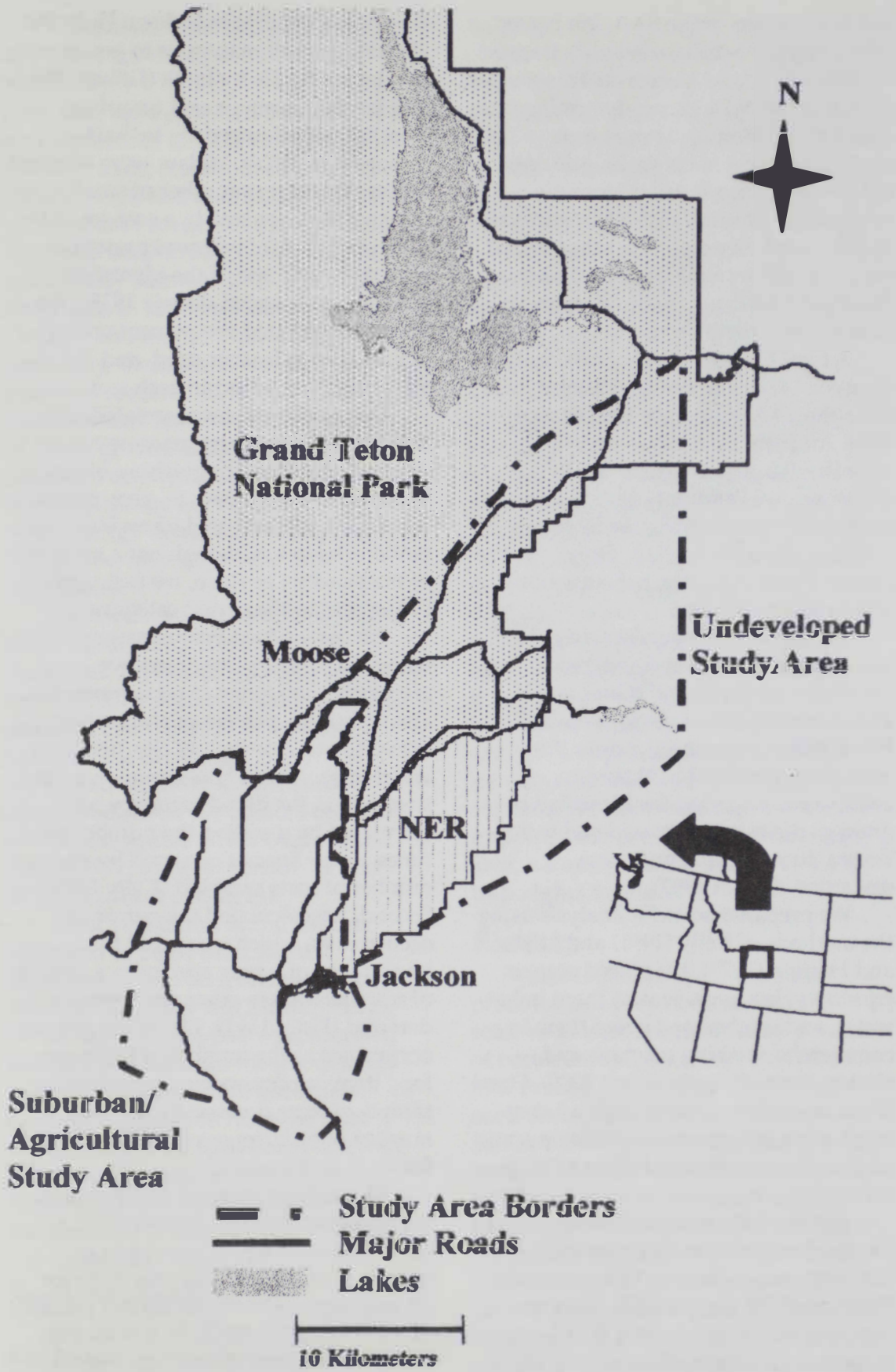

Figure 1. *Study Area: Jackson Hole, Wyoming. NER refers to the National Elk Refuge.*

and 1.4 - 3.6 km in the SAA. We placed scats in paper bags labeled with transect location, date, and Universal Transverse Mercator (UTM) location determined by a Global Positioning System unit (GPS12, Garmin Inc., Olathe, KS). We did not walk transects when snow covered the ground. Instead, scats were opportunistically collected when found on top of the snow in both study areas. Scats were air dried in the summer and frozen during winter.

A total of 786 scats was collected on transects, 476 from the UNDA and 310 from the SAA, from July 1998 to August 1999. An additional 100 scats were opportunistically collected. From this collection, we randomly selected and analyzed 170 scats from the SAA and 169 scats from the UNDA. Only opportunistically collected scats from winter were analyzed.

We identified coyote scats by size and consistency when compared to red fox (*Vulpes vulpes*), wolf (*Canis lupus*), and domestic dog feces (Weaver and Fritts 1979, Green and Flinders 1981). Scats that contained > 50 percent commercial dog food (as identified by grain particles) were considered to be from a domestic dog and were discarded (Quinn 1997).

We prepared scats for analysis using the methods of Kelly (1991) and Johnson and Hansen (1979). We placed scats in rip stop nylon bags, soaked them in hot water, and washed and dried them in a commercial washing machine and clothes dryer (Wigglesworth 2000). Once dried, we sifted scats through a 1-mm mesh sieve to separate identifiable scat residue from particles of dirt and fecal matter.

Aware of the potential biases involved with determining an animal's diet from scat dissection (Weaver and Hoffman 1979, Andelt 1985, Kelly and Garton 1997, Wigglesworth 2000), we analyzed scats using the methods of Murie (1935) and Weaver (1977) to compare our results with previous coyote diet studies in Jackson Hole. We identified small mammals to genus and species primarily by teeth (Gilbert 1980), and larger mammals and ungulates were identified primarily by hair (Moore *et al.* 1974). Molars were counted so that the largest number of small mammals recognized in a scat could be identified. If only hair was present in a scat, then only one of the identified species was counted (Murie 1935). We visually estimated the percent volume of hair, insect, feather, seed, and vegetation contained in each scat.

Due to difficulties associated with hair identification and inaccuracy associated with distinguishing bison from cattle hair (T. Moore, pers. comm.), we combined cattle and bison into the bovid category. Although not a member of the Family Cervidae, we included pronghorn in the cervid category.

We determined prey consumption using two calculations. First, we calculated frequency of occurrence, i.e., also known as percent of scats when converted to a percent (Kelly 1991), which represented how common a prey item was in the diet. Frequency was calculated by dividing the number of times a prey species occurred by the number of scats sampled (Kelly 1991). Second, we calculated the percent of occurrences, which measured the importance of a prey species in a sample of scats relative to other prey species detected (Kelly 1991). We define percent occurrence as the number of times one food item or prey species occurred in a sample of scats divided by the total number of occurrences of all food items found in that sample.

We analyzed percent and frequency of occurrence by defining occurrence as the presence of a prey species in a sample of scats, and this was done for all prey types. We also analyzed percent of occurrence for small mammals only using the number of small mammals found per scat as indicated by tooth counts (Wigglesworth 2000).

We analyzed percent and frequency of occurrence data annually and seasonally. We defined three seasons: scats that were collected between July and September of 1998 were called late summer scats; scats collected between October 1998 and mid May 1999 were called winter scats; and scats collected from mid May to August 1999 were called early summer scats. Because snow falls in Jackson Hole as early as October and may not completely melt until May, these seasons reflected potential seasonal differences in prey. Both summer seasons encompass times of Uinta ground squirrel (*Spermophilus aramatus*) activity. Additionally, most coyote pups are born in early May when energy demands are high, and this period may reflect dietary differences.

We used tests for two proportions (95% CI, $\alpha = 0.05$; Reynolds and Aebischer 1991) and chi-square tests ($\alpha = 0.05$), respectively for annual and seasonal comparisons of food items between the SAA and UNDA. We calculated adjusted residuals to determine where differences occurred within chi-square tables (Agresti and Finlay 1997; Minitab version 12 and SPSS statistical packages).

Most vegetation found in scats appeared to be from incidental ingestion or was attached to the scat when it was collected. Additionally, some vegetation appeared macerated and likely came from the gut of small mammalian prey. For these reasons we excluded vegetation from the total occurrences of all food items when we calculated percent of occurrence. However, we did include seeds, which indicated the consumption of berries, in our analyses.

Small Mammal Surveys

We placed Sherman live traps in five habitat types: aspen, conifer, grass, riparian, and shrub. For each study area, four transects, each with five 0.04 ha plots, were randomly placed in each of the five habitat types in summers of 1998 and 1999. One trap was placed at the center of each plot and one at the edge of each plot in the four cardinal directions, totaling five traps/plot. Traps were opened in the evening and checked in the morning after sunrise.

We captured small mammals for a total of 500 trap-nights/study area during each trap session. Trapping sessions lasted two weeks and were conducted in July and September of 1998 and late May-early June and July of 1999. Traps were open during part of the daylight hours to account for diurnal activity of small mammals but were closed during the heat of the day to minimize mortality. Traps were open for two nights at a set of transects and then moved to another set of transects. Trapping transects were located in different habitat patches but were equally dispersed in the five habitat types. Because the numbers of individual small mammal species caught were proportionately similar between the 1998 and 1999 trapping sessions, we combined data for the four trapping sessions. Thus, for each study area, we analyzed the data from 2,000 trap nights together.

Results

Voles (*Microtus* spp.) were the predominant prey item during all seasons in both study areas by percent of occurrences (24% in the UNDA and 49% in the SAA) and by frequency of occurrence (65% UNDA, 91% SAA; Tables 1 and 2). Annually, SAA coyotes consumed significantly more voles than UNDA coyotes as measured by both frequency of occurrence and percent of occurrences (Test of two proportions, $P < 0.01$). Scats collected in the UNDA had a significantly higher frequency of occurrence of bird, insect, seed, pocket gopher, and cervid remains than scats from the SAA (Test of two proportions, $P \leq 0.01$). We found similar results when

Table 1. *Percent occurrence of prey items found in coyote scats in undeveloped (UNDA; n = 169) and suburban/agricultural (SAA; n = 170) areas of Jackson Hole, Wyoming, July 1998 to August 1999. Sample sizes are also indicated.*

	Annual		Late summer July - Sept '98		Winter: Oct '98 - May '99		Early summer: May - Aug '99	
Food Item[1]	UNDA	SAA	UNDA	SAA	UNDA	SAA	UNDA	SAA
Mammals	62.4*	72.0*	53.2	60.2	63.2*	80.8*	71.8	77.9
Small Mammals	45.7*	58.8*	43.5	53.4	38.7*	63.5*	55.8	61.1
Vole	23.5*	48.7*	20.1*	44.9*	24.5*	56.7*	26.3*	45.3*
Pocket Gopher	15.8*	7.5*	17.5*	7.6*	9.7	4.8	20.5*	10.5*
Ground Squirrel	2.4	1.9	0.6	0.8	1.9	1.0	4.5	4.2
Chipmunk	2.1	-	2.6	-	1.9	-	1.9	-
Jumping Mouse	1.1	-	1.9	-	-	-	1.3	-
Deer Mouse	0.4	-	0.6	-	0.6	-	-	-
Red Squirrel	0.2	-	-	-	-	-	0.6	-
Red-backed Vole	0.2	0.3	-	-	-	-	0.6	1.1
Water vole	-	0.3	-	-	-	1.0	-	-
Ungulates	14.7*	9.1*	7.8	3.4	22.6*	12.5*	14.1	12.6
Cervids	10.5*	5.0*	5.2	1.7	16.8*	8.7*	9.6	5.3
Bovids	4.3	4.1	2.6	1.7	5.8	3.8	4.5	7.4
Other Mammals	1.9	4.1	1.9	3.4	1.9	4.8	1.9	4.2
Weasel	0.5	-	0.6	-	-	-	0.6	-
Porcupine	0.6	0.6	0.6	-	1.3	1.0	-	1.1
Skunk	-	0.3	-	-	-	1.0	-	-
Beaver	-	0.6	-	-	-	1.9	-	-
Coyote	0.2	0.9	-	1.7	0.6	-	-	1.1
Canid	0.6	0.6	0.6	0.8	-	1.0	1.3	-
Raccoon	-	0.3	-	-	-	-	-	1.1
Black Bear	-	0.3	-	-	-	-	-	1.1
House Cat	-	0.3	-	0.8	-	-	-	-
Birds	5.1	3.1	6.5	4.2	3.2	2.9	5.8	2.1
Insects	16.0*	9.4*	20.8	13.6	12.3*	3.8*	15.4	10.5
Seeds	12.2	10.7	14.8	16.9	15.5	8.7	6.3	5.2
Unknown	2.6	4.4	4.5	5.1	2.6	3.8	0.6	4.2
Human-Related	1.7	0.3	0.7	-	3.2	-	1.3	1.0
Sample size	169	170	47	53	69	68	53	49

[1] Scientific names of prey species not referred to in the text: Chipmunk (*Tamias* spp.), red squirrel (*Tamiasciuris hudsonicus*), red-backed vole (*Clethrionomys gapperi*), water vole (*Microtus richardsoni*), weasel (*Mustela erminea, Mustela frenata*), porcupine (*Erithizon dorsatum*), skunk (*Mephitus mephitus*), beaver (*Castor canadensis*), raccoon (*Procyon lotor*), black bear (*Ursus americanus*)

* Significant differences between the SAA and UNDA within each season, Test of two proportions, $P < 0.05$

scats were analyzed by percent of occurrences (Test of two proportions, $P \leq 0.05$), with the exception that there were no significant differences between the two areas in bird remains and seeds found in scats. Chipmunk (*Tamais* spp.) remains were found only in scats from the UNDA. Insects (21%) occurred at similar percents as voles (20%) during the late summer in the UNDA (Table 1).

By use of percent occurrences, we found a higher proportion of mammals present in the SAA scats than the UNDA scats when all mammals were combined (Test of two proportions, $P < 0.05$; Table 1). Scats from the SAA had a higher proportion of small mammals (rodents) than the UNDA, and scats from the UNDA had a higher proportion of large mammals

Table 2. *Frequency of occurrence (expressed in percents) of prey items found in coyote scats in undeveloped (UNDA; n = 169) and suburban/agricultural (SAA; n = 170) areas of Jackson Hole, Wyoming, July 1998 to August 1999.*

	Annual		Late summer: July - Sept '98		Winter: Oct '98 - May '99		Early summer: May - Aug '99	
Food Item	UNDA	SAA	UNDA	SAA	UNDA	SAA	UNDA	SAA
Vole	65.1*	91.2*	66.0*	100.0*	55.1*	86.8*	77.4	87.8
Pocket Gopher	43.8*	14.1*	57.4*	17.0*	21.7*	7.4*	60.4*	20.4*
Ground Squirrel	6.5	3.5	2.1	1.9	4.3	1.5	13.2	8.2
Chipmunk	5.9	-	8.5	-	4.3	-	5.7	-
Jumping Mouse	3.0	-	6.4	-	-	-	3.8	-
Deer Mouse	1.2	-	2.1	-	1.4	-	-	-
Red Squirrel	0.6	-	-	-	-	-	1.9	-
Red-backed Vole	0.6	0.6	-	-	-	-	1.9	2.0
Water vole	-	0.6	-	-	-	1.5	-	-
Cervids	29.0*	9.4*	17.0	3.8	37.7*	13.2*	28.3*	10.2*
Bovids	11.8	7.6	8.5	3.8	13.0	5.9	13.2	14.3
Weasel	1.2	-	2.1	-	-	-	1.9	-
Porcupine	1.8	1.2	2.1	-	2.9	1.5	-	2.0
Skunk	-	0.6	-	-	-	1.5	-	-
Beaver	-	1.2	-	-	-	2.9	-	-
Coyote	0.6	1.8	-	3.8	1.4	-	-	2.0
Canid	1.8	1.2	2.1	1.9	-	1.5	3.8	-
Raccoon	-	0.6	-	-	-	-	-	2.0
Black Bear	-	0.6	-	-	-	-	-	2.0
House Cat	-	0.6	-	1.9	-	-	-	-
Bird	14.2*	5.9*	21.3	9.4	7.2	4.4	17.0	4.1
Insect	44.4*	17.6*	68.1*	30.2*	27.5	5.9	45.3*	20.4*
Seed	33.7*	20.0*	48.9	37.7	34.8*	13.2*	18.9	10.2
Unknown	7.1	8.2	14.9	11.3	5.8	5.9	1.9	8.2
Human Related	4.7	0.6	2.1	-	7.2	-	3.8	2.0
Sample size	169	170	47	53	69	68	53	49

* Significant differences between the SAA and UNDA within each season, Test of two proportions, $P \leq 0.05$.

(ungulates). Coyotes in the UNDA consumed higher proportions of cervids, pocket gophers, and insects, and the SAA coyotes consumed a higher proportion of voles (Table 1).

We found fewer between-area differences in diets of coyotes in the two study areas when prey remains in scats were compared seasonally by percent occurrence. During all seasons voles were significantly more common in the diet of SAA coyotes than UNDA coyotes. Coyotes from the UNDA ate a significantly higher proportion of pocket gophers (*Thomomys talpoides*) during both summer seasons and ate significantly more cervids than SAA coyotes only during the winter season. Coyotes from the UNDA ate significantly more insects than SAA coyotes during the winter, however due to small sample sizes the normal approximation may have been inaccurate (Test of two proportions, $P \leq 0.05$; Table 1).

The diet of coyotes from each study area varied seasonally. Seasonal differences in prey items found in the diet were determined with chi-square contingency tables and adjusted residuals. Seasonally, by frequency of occurrence, UNDA coyotes had a significantly higher frequency of voles in their diet in early summer and a

lower frequency in winter, although the *P*-value was marginal (Table 2; $\chi^2 = 7.57$, 2 d.f., $P = 0.048$; adjusted residuals > |2|). Chi-square tests were unreliable for frequency of voles found in SAA scats because of cell counts <5. However, coyotes consumed a higher frequency of voles in late summer than expected ($\chi^2 = 7.57$, 2 d.f., $P = 0.023$; adjusted residuals > |2|). We found no seasonal difference in pocket gopher remains in scats in the SAA but found a higher frequency of pocket gophers in both summer seasons than in the winter season in the UNDA ($\chi^2 = 22.50$, 2 d.f., $P = 0.000$; adjusted residuals > |2|). There was a marginal increase in the frequency of cervids found in UNDA scats in the winter, and a decrease in the late summer ($\chi^2 = 6.08$, 2 d.f., $P = 0.048$; adjusted residuals > |2|). As expected, frequencies of seeds in scats were higher in late summer and lower in the early summer (UNDA: $\chi^2 = 10.14$, 2 d.f., $P = 0.006$; adjusted residuals > |2|; SAA: $\chi^2 = 15.10$, 2 d.f., $P = 0.001$; adjusted residuals > |2|). Analysis of percent occurrence data found fewer but similar seasonal differences.

When percent of occurrences of small mammals, as determined by total counts of individual small mammals/scat by tooth count, was analyzed separately from all other food items, voles comprised 96 percent of small mammals eaten by SAA coyotes (Table 3). Voles occurred in more scats from the SAA than the UNDA, but pocket gopher remains were found in more scats from the UNDA (Test of two proportions, $P \leq 0.001$). Coyotes from the UNDA had a higher proportion of Uinta ground squirrels in their diets (Test of two proportions, $P \leq 0.05$). Deer mice (*Peromyscus maniculatus*) occurred in few scats from either study area.

As an indicator of small mammal occurrences in the two study areas, we combined the number of each small mammal species captured in each of five habitat types during the four trapping sessions (Fig. 2). We captured a total of 393 small mammals in the UNDA and 360 in the SAA. More deer mice (66 and 48% of the respective captures in the UNDA and SAA) were caught than any other small mammal, but deer mice comprised <1 percent frequency of occurrence among scats from the UNDA and were not found in SAA scats. Voles comprised 9 percent of the captures in the UNDA and 19 percent in the SAA, and were found in 62 and 96 percent of respecrive scats in the UNDA and SAA (Table 3, Fig. 2).

Jumping mice (*Zapus princeps*) were

Table 3. *Percent occurrence of small mammals by tooth counts in coyote scats in undeveloped (UNDA; n = 169) and suburban/agricultural (SAA; n = 170) areas of Jackson Hole, Wyoming, July 1998 to August 1999.*

	Annual		Late summer: July - Sept '98		Winter: Oct '98 - May '99		Early summer: May - Aug '99	
Food Item	UNDA	SAA	UNDA	SAA	UNDA	SAA	UNDA	SAA
Vole	61.6*	95.8*	55.8*	97.2*	77.8*	97.4*	53.1*	90.6*
Pocket Gopher	30.1*	3.3*	34.7*	2.5*	16.7*	1.8*	38.3*	6.8*
Ground Squirrel	2.9*	0.7*	1.1	0.3	2.4	0.4	4.3	2.1
Chipmunk	2.6	-	4.2	-	2.4	-	1.9	-
Jumping Mouse	1.3	-	3.2	-	-	-	1.2	-
Deer Mouse	0.5	-	1.1	-	0.8	-	-	-
Red Squirrel	0.3	-	-	-	-	-	0.6	-
Red-backed Vole	0.3	0.1	-	-	-	-	0.6	0.5
Water vole	-	0.1	-	-	-	0.4	-	-

* Significant differences between the SAA and UNDA within each season, Test of two proportions, $P \leq 0.05$.

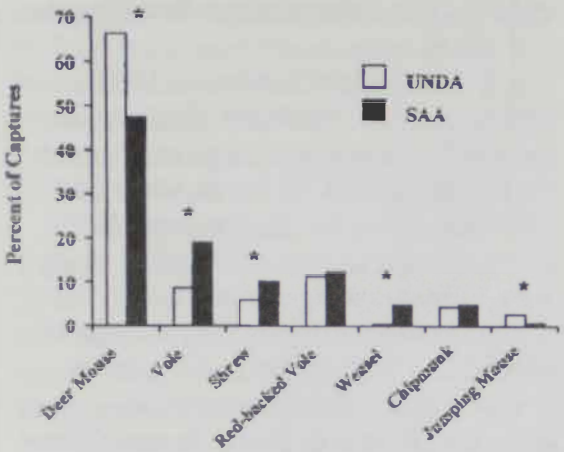

Figure 2. *Percent of small mammals caught during four trap sessions in five habitat types in undeveloped (UNDA) and suburban/ agricultural (SAA) areas of Jackson Hole, Wyoming, July and September 1998 and May- June and July 1999. Asterisks (*) indicate significant differences between the SAA and UNDA (test of two proportions, $P < 0.05$; the normal approximation may be inaccurate for the weasel and jumping mouse due to small samples).*

captured only during the 1999 trapping sessions (1 and 8% of the respective SAA and UNDA captures). Shrews (*Sorex* spp.) were captured predominantly during the 1998 trapping sessions. In 1998 shrews comprised 18 and 9 percent of respective SAA and UNDA captures, but they comprised only 1 percent of the captures in 1999 in both the UNDA and SAA. We captured significantly more deer mice in riparian habitats than in grass and aspen habitats in the UNDA and significantly more in conifer and shrub than grass habitats in the SAA (one-way ANOVA, Tukey's pairwise comparison family error rate of 0.05 and Tamhane's T2 test).

We did not detect garbage or human related foods frequently in any of the scats. Items that we detected included cloth, string, tin foil, plastic, and shotgun pellets. We found a claw from a domestic cat in a scat from the SAA in the late summer season.

Discussion

The results from this study were similar to results from previous studies of coyote diets in Jackson Hole, Wyoming. Like Murie (1935) and Weaver (1977), we found that voles were important prey items for coyotes. Additionally, because we caught more deer mice than voles in both study areas, coyotes apparently were selecting voles more than expected and deer mice less than expected. We could not validate this conclusion because low deer mice counts in scats precluded a valid chi-square test. When data from both study areas were combined, voles accounted for only 14 percent of captures in small mammal traps but were the predominant prey item in the diet of coyotes in both areas. The opposite was true for deer mice. We detected 10,673 vole teeth but only six deer mice teeth in the 339 scats we examined. Similarly, Murie (1935) and Weaver (1977) found few deer mice in the diets of coyotes.

Murie (1935) and Weaver (1977) also found a discrepancy between deer mice availability and presence in the diet of coyotes. Reichel (1991) found that coyotes ate few deer mice in proportion to their availability in Montana and concluded that voles were more vulnerable to coyote predation than deer mice. He also noted studies that have shown that deer mice may be easier for researchers to capture than voles.

Our small mammal capture methods were biased toward capturing more deer mice than voles. Voles are more diurnal than deer mice, which are primarily nocturnal, and voles tend to travel along runways they have created (Streubel 1989). The disproportionate amount of deer mice we captured relative to voles is partially explained by the fact that we captured small mammals primarily at night and at fixed locations not necessarily near vole runways.

The presence of voles in the diet of coyotes may be elevated because voles tend to be vulnerable to predation by coyotes that display both diurnal and nocturnal hunting patterns (Streubel 1989). Higher susceptibility of deer mice to trapping also may have elevated the true abundance of deer mice in relation to voles. However, we do not believe that this completely accounted for the absence of deer mice in the diet of coyotes. In years when both voles and deer mice were abundant, coyotes selected for voles (Hamlin *et al.* 1984). Vole populations tend to be cyclic (Streubel 1989); thus, the presence of voles in the diets of coyotes likely would change during vole population highs and lows. Hamlin *et al.* (1984) found that when vole populations were low, coyotes ate proportionally more deer mice than they did when vole populations were high. The duration of our study precluded a determination of vole population cycles.

Voles prefer habitats with dense and abundant grasses (Streubel 1989). Our ground cover measurements found no significant differences in percent grasses between the two study areas with the exception that riparian habitats in the SAA had significantly higher grass cover than riparian habitats in the UNDA (Wigglesworth, unpublished data). Wigglesworth (unpublished data) also found no difference between the two study areas in the amount of dimensional ground cover (vegetation that grew taller than 2.54 cm). However, the UNDA, which had only limited cattle grazing and sporadic grazing by bison, may have provided more cover for voles than the SAA, parts of which were regularly grazed by cattle. Likewise, cover for small mammals was reduced to a minimum when hay was cut on agricultural lands in mid summer. Thus, any differences in cover that might have existed between the two study areas may not explain the difference in vole presence between the two areas.

Although McClure *et al.* (1995) concluded that coyotes in a suburban area of Arizona might have consumed more human-related foods, we found little evidence of anthropogenic foods in the diet of coyotes from either study area. Our sampling methods and difficulty in identifying hair may have limited our finding domestic pets in scat samples. Likewise, our scat collection routes in the SAA, mostly on ranches, may not have been located where scats containing human-related foods would be deposited. Coyotes in Jackson Hole may not need foods directly related to humans but eat prey animals that have increased as a result of human presence and disturbance. Shargo (1988) found that suburban areas of Los Angeles had high prey abundance, and McClure *et al.* (1995) noted a higher number of rodents in areas influenced by human development. Because we captured significantly more voles in the SAA than the UNDA, we speculate that coyotes from the SAA were approaching developed areas to forage for small mammals of which abundance may have increased due to human presence.

Coyotes from the UNDA ate more cervids than did coyotes in the SAA. Because mule deer are not very abundant in the UNDA, most of the cervids detected in the scats likely were elk. However, mule deer, moose, and pronghorn were possibilities. Elk were likely more abundant in the UNDA than the SAA, and many elk carcass remains were left in the UNDA during the annual fall hunt. Consumption of elk likely was in the form of carrion. We did not observe coyotes preying upon cervids although we did witness them chasing pronghorn in the spring, and occasionally elk on the National Elk Refuge. Wells and Bekoff (1982) reported similar observations in the

same area. We speculate that bovid hair in SAA scats were from cattle, and bovid hair from UNDA scats were from bison. No cattle died during their limited grazing allotment in the UNDA, and bison are not found in the SAA.

The high percent occurrence of insects is likely a misrepresentation. Small remains of insects (grasshoppers and beetles) and seeds were found in many scats, however, insects and seeds each comprised on average <4 percent by volume of each scat. We attempted to separate insects into categories of grasshopper and beetle although often finding only pieces of insect exoskeletons in scats made identification difficult. However grasshoppers were present in more scats than were beetles. We found carrion beetles infrequently, but those we could identify were not counted separately from other beetles. Notably, some scats were comprised of almost all insects indicating that insects can be an important supplement to the diet of coyotes in Jackson Hole.

The coyote is a generalist predator capable of switching prey items when the population of one prey species declines (Johnson and Crabtree 1999). Coyotes in the UNDA ate voles and pocket gophers in the summer and supplemented their diet in late summer with insects as availability increased and berries as they ripened. Other studies have shown seasonal dietary changes due to food availability (Bowen 1981, Andelt 1895, Gese *et al.* 1988, Toweill and Anthony 1988, Quinn 1997). In winter coyotes took advantage of ungulate carrion. They also consumed cervids in early summer during the calving season. Scat analysis indicated a drop in cervids in the diet from winter to early summer accompanied by an increase in pocket gophers. Coyotes from the SAA took advantage of abundant voles. This area receives less snowfall than the UNDA, which may make prey acquisition easier. Relative occurrence of voles in the diet of coyotes was highest in the winter. Coyotes from the SAA also increased their consumption of cervids in winter and early summer when such animals were easier to obtain for food.

High-density development has the potential to decrease natural prey items, which in turn could cause coyotes to seek human-related foods. This does not appear to have occurred in developed areas of Jackson Hole, Wyoming. Human development appeared to have little effect on the diet of coyotes in suburban/agricultural areas when compared to the diet of coyotes in an adjacent undeveloped area. Pockets of high and low-density developments exist in the SAA, but they are interspersed with agricultural areas and open spaces and are surrounded by public lands. Natural prey items may be sufficiently abundant due to open spaces found within the SAA that coyotes have little need to forage for anthropogenic food sources.

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