Coyote space use in relation to prey abundance

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Received June 18, 1990

MILLS, L. S., and KNOWLTON, F. F. 1991. Coyote space use in relation to prey abundance. Can. J. Zool. **69**: 1516–1521.

Food abundance is an important factor determining space use in many species, but its effect on carnivore home range and territory size has rarely been investigated. We explored the relationship between food abundance for the coyote (*Canis latrans*) and space use in two study areas in the northern Great Basin, where the primary prey, the black-tailed jackrabbit (*Lepus californicus*), fluctuates dramatically in abundance. At one site, home ranges and territories were significantly larger during a time of prey scarcity than when prey was abundant. Coyotes on the second site had similar-size home ranges and territories at low and high prey abundance, but a higher proportion and probably a higher number of individuals were transients during the prey-scarcity period. We propose mortality rates of coyotes as an important factor mediating adjustments in space use to food abundance, and suggest two mechanisms by which mortality might interact with food abundance. Higher mortality rates may simply permit more rapid adjustment of home range size to changing food conditions. Alternatively, higher mortality may selectively eliminate transients, thus reducing the impact of intruders in limiting the size of the remaining territories.

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L'abondance de nourriture est un facteur déterminant de l'utilisation de l'espace chez plusieurs espèces, mais son influence sur l'envergure du territoire ou du domaine vital d'un carnivore a rarement été étudiée. Nous avons examiné, chez le coyote (*Canis latrans*), la relation entre l'abondance de nourriture et l'utilisation de l'espace en deux régions de la partie nord du Grand Bassin où il y a une fluctuation considérable de l'abondance de sa proie principale, le lièvre de Californie (*Lepus californicus*). À l'un des deux endroits, le domaine vital et les territoires se sont avérés significativement plus grands durant une pénurie de proies que durant les temps d'abondance. Les coyotes du second site avaient des domaines vitaux et des territoires semblables en temps de pénurie et en temps d'abondance, mais il y avait une plus grande proportion, et probablement aussi un plus grand nombre absolu, d'individus de passage durant la période de pénurie. Nous croyons que les taux de mortalité des coyotes constituent un important facteur d'ajustement de l'équilibre entre l'utilisation de l'espace et l'abondance des proies et nous indiquons deux mécanismes d'interaction possibles entre la mortalité et l'abondance de nourriture. Des taux de mortalité élevés peuvent simplement permettre un ajustement plus rapide du domaine vital aux modifications des ressources alimentaires. D'autre part, une mortalité plus importante peut éliminer les individus de passage de façon sélective, ayant pour effet de limiter l'impact des intrus dont la présence réduit les dimensions des territoires encore disponibles.

[Traduit par la rédaction]

Introduction

Food abundance may influence the use of space by many vertebrates. For example, an inverse relationship between food abundance and home range size has been reported for fish (Slaney and Northcote 1974), lizards (Simon 1975), birds (Hixon et al. 1983; Griffin and Baskett 1985), and small mammals (Mares et al. 1982). In addition, the expression of territorial behaviour may depend upon food abundance (Gill and Wolf 1975; Carpenter and MacMillen 1976), and space use may be determined by complex interactions between food resources and other factors (e.g., Myers et al. 1979, 1981; Ruby and Dunham 1987).

Little is known about how the use of space by carnivores changes in relation to prey abundance, partly because of the logistics of capture, the difficulty of manipulating their food resources, and the array of behavioural responses available to these mammals (Gittleman and Harvey 1982; Lott 1984). Because coyotes (*Canis latrans*) are particularly plastic in their behaviors (Bekoff and Wells 1986), investigation of their use of space in relation to prey abundance is especially interesting.

Coyotes exhibit territorial spacing, with both defence and exclusive use of areas (Camenzind 1978; Bowen 1981; Messier and Barrette 1982; Andelt 1985; Windberg and Knowlton 1988). Their territoriality is not obligate (see Bekoff and Wells 1986), and the role of food in its expression is unknown (Lott 1984). With regard to size of coyote territories, means range from <2.5 km^2 in south Texas (Andelt 1985; Windberg and Knowlton 1988) to ≥ 15 km^2 in northern parts of their range (Bowen 1982; Harris 1983; Roy and Dorrance 1985), but there is no consensus on how the size of areas used varies with prey abundance (Camenzind 1978; Kleiman and Brady 1978; Messier and Barrette 1982; Bekoff and Wells 1986; Gese et al. 1988).

We examined space-use patterns of free-ranging coyotes in relation to prey abundance in the northern Great Basin, where black-tailed jackrabbits (*Lepus californicus*) vary greatly in abundance over time (Wagner and Stoddart 1972; Gross et al. 1974). In this area, lagomorphs comprise 65 to 90% of the coyote diet, with rodents representing most of the balance (Clark 1972; Hoffman 1979; Johnson and Hansen 1979). We assessed coyote spacing patterns in years of high and low prey abundance, while study site, time of year, and study methods were unchanged. Specifically, we tested the hypothesis that coyote home range and (or) territory size increases when prey abundance decreases. Both home range and territory sizes were considered because interactions between individuals and the environment may differ according to the intensity of use of the area (Samuel et al. 1985*b*). We also examined whether territoriality might be

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Printed in Canada / Imprimé au Canada

abandoned at low prey abundance. These questions were studied at two sites that differed in coyote mortality rates.

Study areas

Coyote space use and prey abundance were monitored at two sites separated by about 150 km in the Great Basin of northern Utah and southern Idaho.

Curlew Valley

The Curlew Valley area encompasses approximately 400 km^2 in northern Utah. Vegetation is dominated by sagebrush (*Artemisia tridentata*) and greasewood (*Sarcobatus vermiculatus*) communities (Clark 1972; Gross et al. 1974). The principal mammalian fauna of Curlew Valley includes the coyote, badger (*Taxidea taxus*), red fox (*Vulpes vulpes*), bobcat (*Lynx rufus*), mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), black-tailed jackrabbit, and at least 20 rodent species. Coyotes in the area are heavily exploited by aerial and ground hunting and by trapping. Davison (1980) reported that 70–75% of all marked coyotes died as a result of human exploitation.

In Curlew Valley, 1981 was a year of high jackrabbit abundance, while the period of 1985 and 1986 was one of low abundance (Stoddart 1987*a*[2]). In 1981, 331 and 342 jackrabbits were counted on 65 transects in spring and autumn, respectively; density estimates were, respectively, 136 and 168 jackrabbits/km^2. During spring and fall of 1986, only five and four jackrabbits, respectively, were counted on 63 of the same transects; samples were too few to calculate density estimates.

Rodent abundance, as monitored by catch per unit effort indices derived from approximately 700 snap-trap nights in 1981 and 1986, followed the same trend as jackrabbit densities (Stoddart 1987*a*[2]; Mills 1987). Density indices taken individually for each of the five most commonly trapped species, the deer mouse (*Peromyscus maniculatus*), Great Basin pocket mouse (*Perognathus parvus*), least chipmunk (*Eutamius minimus*), Ord's kangaroo rat (*Dipodomys ordii*), and western harvest mouse (*Reithrodontomys megalotis*), indicated that each was more abundant in 1981 than in 1986 or not different.

Idaho National Engineering Laboratory

This study area encompassed about 300 km^2 of the Idaho National Engineering Laboratory (INEL) in southeastern Idaho. Vegetation, topography, and climate on the INEL site are typical of sagebrush–grass complexes of the northern cool desert (Harniss and West 1973; Reynolds et al. 1986). Although the site is closed to trespassing, hunting, and trapping by the general public, about a third of the INEL site is occasionally hunted for coyotes. The proportions of marked juvenile and adult coyotes killed by humans on INEL during the study of Davison (1980) were significantly lower than in Curlew Valley: 22 and 51%, respectively.

Principal mammalian fauna on INEL is similar to that of Curlew Valley, except that INEL also has fluctuating populations of cottontail rabbits (*Sylvilagus nuttali* and *Sylvilagus idahoensis*) (Reynolds et al. 1986).

The periods of high and low prey abundance for the INEL portion of this study were 1979 and 1985–1986, respectively. Densities of both jackrabbits and cottontails, based on 22 flushing transects, were greater in 1979 than 1986 (Stoddart 1987*b*[3]). In 1979, 10 jackrabbits were seen in the spring and 44 in the autumn. The spring sample was too small to provide a density estimate but in the autumn it was 32 jackrabbits/km^2. In 1986, no jackrabbits were seen in either spring or autumn. Cottontail densities on INEL followed a similar a similar trend; 19 and 28 cottontails, respectively, were sighted in the spring and autumn of 1979, yet none were sighted in 1986.

Rodent abundance indices from snap-trap lines for the five most commonly trapped rodent species on INEL suggest that rodents were at similar or lower abundances in 1986 relative to 1979 (Stoddart 1987*b*[3]). This conclusion is supported by another study in which autumn rodent densities on INEL, as assessed by museum special snap traps, were not significantly different ($P > 0.05$) in 1980 and 1986 (B. Keller, personal communication).

Methods

Coyote space use during a period of high prey abundance was assessed in Curlew Valley, based on about 200 h of radio-tracking from mid-June to mid-July 1981 (F. F. Knowlton, unpublished data), and in INEL, based on about 80 h from late August to mid-September 1979 (Harris 1983). We collected data on periods of low prey abundance in 1985 and 1986, during the same time of the year and with the same intensity that data on high prey abundance were collected in each study site. In INEL in 1985, preliminary searches indicated that all captured coyotes were behaving as transients; therefore no extensive radio-tracking effort was initiated.

Coyotes were captured with either a helicopter and tranquilizer gun, or leg-hold traps with tranquilizer tabs (Balser 1965). Radio-collared coyotes were monitored by triangulation from fixed radiotelemetry stations with an average angular error of 1.3° (Mills and Knowlton 1989). To ensure valid comparisons of spacing patterns (Laundré and Keller 1984), monitoring schedules were similar during the two periods within each study area. Effects of sample size and serial correlation (Dunn and Gipson 1977; Bekoff and Mech 1984; Swihart and Slade 1985*a*, 1985*b*) were minimized for comparisons between periods of high and low prey abundance by standardizing the minimum time interval between successive locations so that it was the same for both periods within a study site.

Core areas and home ranges were calculated using a modified harmonic mean estimator (program HOME RANGE, Samuel et al. 1985*a*). A core area was defined by the harmonic probability contour exceeding a uniform utilization distribution (Samuel et al. 1985*a*, 1985*b*). For the purpose of this paper, the core area is considered equivalent to "territory," and the area encompassed by the 85% contour of the UD defines the "home range."

The program HOME RANGE also identified "outliers," the extreme locations resulting from animals moving beyond their usual activity areas. For each animal, percent outliers was calculated as the number of outliers relative to the total number of locations. Where territories are contiguous, the percentage of outliers provides an index to the intrusions that radio-collared animals make into neighboring territories. Outliers were excluded from home-range and core-area size determinations (Samuel and Garton 1985; Samuel et al. 1985*a*, 1985*b*).

The effect of prey abundance on core area and home range sizes, and on the percentage of outliers, was assessed with an analysis of covariance (ANCOVA) for unbalanced data (Wilkinson 1988). Data from 1985 and 1986 were pooled for the period of low prey abundance. Because telemetry data were collected to establish a comparison, within each study site, across periods of differing prey abundance, the main factors in the ANCOVA model were prey abundance and site. Two other factors, sex and age, were considered covariates because they may affect space use but were not controlled in the sampling design. Preliminary model runs with age as a covariate indicated no effect of age and little reduction in the residual sum of squares, so the final ANCOVA model included sex but not age as a covariate.

Results

Individual coyotes showed either territorial or transient spatial patterns. Coyotes that were considered territorial occupied relatively discrete home ranges with exclusive core areas (Messier and Barrette 1982; Lott 1984; Bekoff and Wells 1986). Two females radio-tracked in Curlew Valley during the period of low prey abundance were infrequently triangulated because of topographic constraints, but were inferred to be territorial because they were lactating when captured and were observed with mates that had discrete areas of use. Telemetry data from

[2]Stoddart, L. C. 1987*a*. Relative abundance of coyotes, lagomorphs, and rodents in Curlew Valley, Utah. Fin. Rep. Denver Wildl. Res. Cent. USDA APHIS ADC, Denver, CO.

[3]Stoddart, L. C. 1987*b*. Relative abundance of coyotes, lagomorphs, and rodents on the Idaho National Engineering Laboratory. Fin. Rep. Denver Wildl. Res. Cent. USDA APHIS ADC, Denver, CO.

TABLE 1. Spatial patterns used by coyotes radio-tracked in Curlew Valley, northern Utah, and in INEL, southeastern Idaho, during periods of high and low prey abundance

	Curlew Valley			INEL		
	High prey abundance, 1981	Low prey abundance 1985	Low prey abundance 1986	High prey abundance, 1979	Low prey abundance 1985	Low prey abundance 1986
Number of radio-tracked coyotes	7	5	8	5	10	8
Number of transients						
Males	1	1	1	0	7	1
Females	1	2	1	0	3	3
Total	2	3	2	0	10	4
% transients among captures	29	38		0	78	

TABLE 2. Means of space use variables for territorial coyotes in Curlew Valley and INEL

Prey abundance	No. of coyotes	Area (km^2) Territory	Area (km^2) Home range	Percent outliers
Curlew Valley				
High abundance	5	8.1 (1.7)	17.6 (4.0)	2.2 (1.6)
Low abundance	6	19.8 (4.4)	39.0 (9.0)	4.7 (2.1)
INEL				
High abundance	5	5.5 (0.9)	11.5 (2.0)	4.4 (1.1)
Low abundance	4	5.0 (1.4)	12.3 (3.6)	4.5 (0.5)

NOTE: Areas within harmonic mean utilization contour were provided by the computer program HOME RANGE (Samuel et al. 1985*a*). Data in parentheses are standard errors.

these two coyotes were not included in space-use calculations. All other animals that were considered territorial were located on an average of 83% of the attempts in Curlew Valley and 84% of the attempts in INEL.

In contrast to territorial animals, transients were those whose locations were widely dispersed among and between the core areas of other coyotes (e.g., Pyrah 1984; Andelt 1985; Windberg and Knowlton 1988). Because the nomadic movements of transients resulted in infrequent localizations (on average 21% of attempts in Curlew Valley and 9% in INEL), we did not quantify space use for these animals.

In Curlew Valley, the proportion of transient to territorial coyotes did not differ between populations during the periods of high and low prey abundance (Table 1, Fisher's exact test, $P = 0.7$). During the high-abundance period, 29% (2/7) of the captured coyotes were transients versus 38% (5/13) during the low-abundance period.

In INEL, the proportion of transient to territorial coyotes was significantly greater during the period of low prey abundance than during the high-abundance period (Table 1, Fisher's exact test, $P < 0.001$). There were no transients in the high-abundance period (0/5), whereas in the low-abundance period, 78% (14/18) of all captured coyotes were transients. Age or sex of coyotes does not explain these differences, because age and sex composition of instrumented INEL coyotes were comparable between periods of high and low prey abundance periods of high and low (Fisher's exact test, $P > 0.5$).

Statistical analyses of space use were based on territorial animals, for which we had relatively large numbers of telemetry locations. In the period of high prey abundance, 10 territorial coyotes were located 170–366 ($x = 266$) times. The 10 territorial coyotes of the low-abundance period were located 127–264 ($x = 191$) times. The ANCOVA models, which tested for effect of periods of differing prey abundance on territory (core area) and home range sizes, and on the percentage of outliers, showed no serious departures from normality (Lilliefors test, $P > 0.05$). Sex was not a significant covariate ($P > 0.08$) for any of the variables.

Based on the ANCOVA, territory and home range sizes were significantly different ($P = 0.03$ and 0.04, respectively) between the two differing prey-abundance periods. The study site also had a main effect on territory ($P = 0.03$) and home range sizes ($P = 0.05$), although biological significance cannot be attributed to this effect because data collection and analysis methods were different among study areas. The significant prey-abundance period by site interactions for both territory ($P = 0.02$) and home range sizes ($P = 0.04$) indicate that these variables changed with prey abundance in a site-specific manner.

To separate the interacting effects of site and prey abundance, the ANCOVA model was run for each study area, with prey abundance as a main effect and sex again partitioned as a covariate. In Curlew Valley (Table 2), coyotes had significantly smaller territories ($F = 18.1$, $P = 0.003$) and home ranges ($F = 12.4$, $P = 0.008$) during the period of high prey abundance than during the low-abundance period. These trends did not hold for the INEL site, where no differences ($P > 0.8$) were found between the two periods for either territory or home range size (Table 2).

The other space-use variable examined, percentage of outliers of radio-collared coyotes, did not change on either study area between the periods of high and low prey abundance ($P > 0.5$, Table 2).

Discussion

Two major hypothesis regarding space use in relation to prey abundance were examined in this study.

The first hypotheses was that the size of home ranges and of territories varies inversely with prey abundance (Brown and Orians 1970; Gittleman and Harvey 1982; Mace et al. 1983). Adjustments of territory size to changes in prey abundance have been proposed for territorial coyotes (Kleiman and Brady 1978; Camenzind 1978; Bekoff and Wells 1986). In our study, territorial coyotes in Curlew Valley did have larger home range and territory sizes when prey abundance was low, but coyotes in INEL did not.

The second hypothesis addressed whether low food abundance

affects the incidence of territoriality in coyote populations. In some nectar-feeding birds, territoriality is abandoned when food defence becomes uneconomical during periods of food scarcity (Gill and Wolf 1975; Carpenter and MacMillen 1976). Among carnivores, lions (*Panthera leo*; Packer 1986) and wolves (*Canis lupus*; Messier 1985) may temporarily leave territorial groups and live as transients during periods of prey scarcity. Facultative territoriality in brown hyenas (*Hyaena brunnea*) is also related to prey abundance (Owens and Owens 1979). Although it is well accepted that coyotes can be territorial or transient and can change status over time (Camenzind 1978; Andelt 1985; Bekoff and Wells 1986; Gese et al. 1988; Windberg and Knowlton 1988), prey abundance has not been directly linked to the expression of these behaviours.

In our study, low prey abundance did not consistently result in transients comprising a larger proportion of the population. The period of low prey abundance was accompanied by little change in proportions of transients in Curlew Valley but an increased proportion of transients in INEL.

Although this study could not determine whether the apparent increased proportion of transients in INEL implied an increased absolute number of transients, two independent coyote abundance indices indicate that there was, in fact, an increased number of transient coyotes in INEL when prey abundance was low (Mills 1987). Scat counts and scent station indices (Linhart and Knowlton 1975; Roughton and Sweeny 1982) indicate that coyote numbers were significantly lower during the period of low prey abundance in Curlew Valley and higher during this same period in INEL. The higher coyote indices during the low-abundance period in INEL is unexpected, and could be an artifact of the timing of the studies relative to the time lag in coyote—jackrabbit population dynamics (Wagner and Stoddart 1972; Mills 1987). Whatever the reason for their trends, these indices indicate that absolute numbers of transient coyotes in INEL increased when prey abundance was low.

Overall, our results suggest a complex relationship between changes in prey abundance and space-use patterns of coyotes. In Curlew Valley, low prey abundance was accompanied by larger territory sizes and little change in the proportion of transients. In INEL however, during the period of low prey abundance coyotes did not have larger territories but the proportion of transients increased.

These site-specific differences prompt consideration of other factors that may influence the food abundance – coyote space use relationship. It is possible that the differences simply result from telemetry data being collected in June and July in Curlew Valley and in August and September in INEL. For example, pups would differ slightly in age during each of these periods, which could alter social status and space use of adults.

Of the factors intrinsic to the study areas that are most likely to affect the coyote food abundance – space use relationship, the different levels of human exploitation must be considered. We propose two mechanisms by which mortality rates might alter coyote responses to low prey abundance.

The first mechanism is that mortality rates may affect the rate of adjustment of territory size. This presumes a selective advantage for maintaining a territory large enough for periods of food scarcity (Schaller 1972; Carpenter and MacMillen 1976; Davies and Houston 1984; Stamps and Tollestrup 1984). If coyote territories persist for longer than the life of the individuals that occupy them (Andelt 1985; Knowlton et al. 1986), then coyotes with relatively low mortality rates (e.g., INEL) may have territories of stable size for many generations. In Curlew Valley, however, where coyotes are heavily exploited and mortality rates are higher, territory holders may be eliminated, with new individuals reestablishing territories in relation to the prey abundance perceived at the time. In other words, the high mortality rate induces faster adjustments in area usage than would occur otherwise.

A second interpretation of our results accounts for the site-specific changes of both territory size and percentage of transient animals. As previously discussed, low abundance of prey may be associated with abandonment of territories, and the resulting temporary transients may intrude into persisting territories (Messier 1985). Increased density of conspecific intruders such as temporary transients may decrease the size of persisting territories (Lockie 1966; Krebs 1971; Myers et al. 1979, 1981; Boutin and Schweiger 1988). The number of outlier points associated with territorial coyotes in our study did not increase when prey abundance was low, suggesting that territory holders did not increase their rate of intrusions into other territories. Transients, however, were often located within territories of other coyotes. If low prey abundance causes an increase of transient coyotes, then differential mortality of transients between study sites may explain the site-specific differences in both territory size and percentage of transients.

Such differential mortality of transients may result from trapping. There is evidence that transient coyotes may be more vulnerable to trapping than territorial individuals (Hibler 1977; Harris 1983; Windberg and Knowlton 1990). In our study, in 1985, when leg-hold traps were the primary means of capture, transients made up a much higher proportion of the animals captured (13/15 versus 6/16 in 1986; Table 1).

In the highly exploited area, Curlew Valley, our space-use data are consistent with the hypothesis that transients are selectively removed by trapping, lowering intrusion rates and allowing sizes of persisting territories to expand in response to decreased prey abundance. In INEL, the study area not subjected to intense human exploitation, our results are consistent with the related view that low food abundance may increase the number of transients per remaining territory; these transient intruders restrict territorial expansion during low food abundance.

Models of optimal territory size (Hixon 1982; Schoener 1983) include intruder density as a monotonically increasing function of food abundance (e.g., Myers et al. 1979, 1981). Our proposed scenario associating increased intruder density with decreased food abundance may alter the predictions of optimal territory size.

We conclude that consideration of prey abundance alone is not adequate to predict changes in coyote space use. We suggest that examination of the dynamics of space use in relation to changing food abundance should include consideration of mortality patterns, as well as interactions between transient and territorial animals.

Acknowledgements

We thank C. Harris for providing INEL data and J. P. Gionfriddo, T. Spille, S. R. Olmstead, M. Collinge, S. L. Poulson, and K. Gonzalez for field assistance. Early drafts of this paper were improved by comments from G. Fowler, R. Fredrickson, T. Gersel, G. Smith, and C. Stoddart. L. Windberg, F. Messier, and an anonymous reviewer also gave helpful comments on the manuscript. The U.S. Department of Energy provided access to the INEL study area under Interagency Agreement No. DE-AI07-81ID12315. This work was supported by the Denver Wildlife Research Center of the U.S. Fish and Wildlife Service, which

was tranferred to the Animal and Plant Health Inspection Service, U.S. Department of Agriculture, on 3 March 1986.

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