

FORAGING STRATEGY OF A GENERALIST PREDATOR TOWARD A SPECIAL PREY: COYOTE PREDATION ON SHEEP

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Abstract. How predators select domestic relative to wild prey is of relevance to depredation management and presents opportunities to investigate foraging theory as applied to mammalian carnivores. Domestic prey have numerous qualities that should increase their energy value to predators relative to wild prey. However, whether a predator specializes on domestic prey should also depend on the relative importance of energy efficiency and nonfood-related activities to the predator's fitness, as well as the composition of the alternative prey base. We used radiotelemetry, carcass surveys, and fecal analysis to investigate (1) whether breeding coyotes killed sheep disproportionately to sheep abundance, (2) whether coyotes consumed wild prey disproportionately to wild prey abundances, and (3) the effects of sheep abundance on consumption of five principal wild prey. Coyote pairs killed sheep in proportion to sheep abundance within territories, suggesting that coyotes did not specialize on sheep. Occurrences in scats of four small wild mammalian prey were not significantly correlated with abundance of sheep in territories, but occurrence of deer in scats was negatively correlated with abundance of sheep in territories. Small prey generally comprised a minor portion of the coyote diet. During the lambing period, consumption of deer was lower where sheep were available than where they were not and was inversely correlated over time with sheep predation rate. During the non-lambing period, when only larger sheep were present, consumption of deer was similar where sheep were available and where they were not, and there was no significant relationship between monthly consumption of deer and sheep predation rate. Because coyotes did not specialize on sheep, lambs, or any other prey, these results suggest that their foraging strategy emphasized minimizing time spent with food acquisition over maximizing net energy gain.

Key words: *Canis latrans*; coyote; foraging; generalist predator; prey selection; sheep; specialist predator.

INTRODUCTION

Coyote (*Canis latrans*) predation on domestic sheep in North America is an important economic problem for sheep producers (Wagner 1988). Efforts to manage depredation have concentrated on attempts to reduce coyote abundance in sheep-producing areas (Knowlton 1972, Knowlton et al. 1999). Consequently, ecological research related to this problem has focused on coyote demographics (Knowlton 1972, Connolly and Longhurst 1975). However, it has become increasingly clear that sheep depredation is a complex problem and that coyote abundance alone is a poor predictor of kill rates on sheep (Knowlton et al. 1999). Depredation losses vary considerably, both spatially and temporally, and many factors, both ecological and management-related, are likely to affect this variability (Nunley 1995, Knowlton et al. 1999).

Previous studies at the Hopland Research and Ex-

tension Center (HREC), Mendocino County, California, USA, have examined the roles of predator control practices and the coyote social system in determining predation on sheep (Conner et al. 1998, Sacks et al. 1999a, b; Blejwas et al. 2002). Here we examine the foraging strategy of coyotes in this prey-rich environment, with particular emphasis on the role of sheep in the diet of breeding coyotes. We focused on the breeding population as this segment was responsible for most, if not all, sheep depredation at HREC (Sacks et al. 1999b) and elsewhere (Till and Knowlton 1983). Breeding coyotes are socially dominant and have been observed to inhibit access of nonbreeders (e.g., pups, pack associates) to certain foods (Gese et al. 1996a), possibly explaining why nonbreeders avoid predation on even small domestic ungulates.

Although the coyote is an archetypal generalist (i.e., the species as a whole has a broad food niche), coyote populations (O'Donoghue et al. 1998, Patterson et al. 1998) and individuals within populations (Gese et al. 1996b, Sacks et al. 1999b) may specialize to varying degrees on particular prey (see Roughgarden 1974 for a general discussion). In this study, we were concerned with the population-level foraging strategy of coyotes, especially with respect to sheep. Although speciali-

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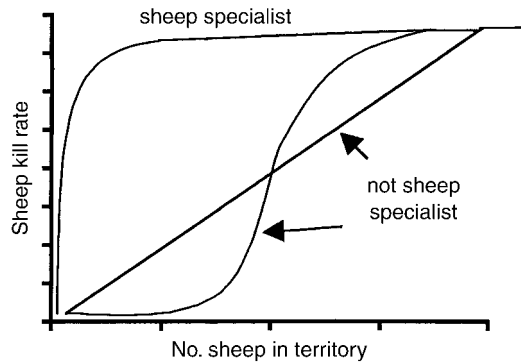


FIG. 1. Three hypothetical relationships between mean coyote predation rate and mean abundance of sheep in a territory. A high, constant predation rate regardless of sheep abundance (above some minimum) indicates that coyotes generally specialize on sheep, whereas a linearly increasing or sigmoid relationship indicates that coyotes generally do not specialize on sheep. Whether coyote populations specialize on sheep is most apparent when territories contain low to moderate sheep abundance.

zation can be defined in many ways, we considered a prey to be "specialized on" by a population if predators with differing abundances (above some minimum) of that prey in their territories preyed on it at similarly high rates (i.e., regardless of abundance; Fig. 1). This definition is the population-level analogue to the type II functional response of an individual predator to changes in a prey's abundance over time.

Whether a breeding coyote population exhibits prey specialization is likely to depend on the relative importance of energy efficiency vs. time spent on non-food-related activities (e.g., territory maintenance) related to the survival and reproductive success of the coyote. Further, to the extent that energy efficiency matters, the degree of specialization should depend on the variety of available prey and their variability with respect to intrinsic energy qualities (e.g., handling time, search time per unit abundance, caloric value). Schoener (1971) coined the terms "energy maximizer" and "time minimizer" to refer to ends of a foraging strategy continuum ranging from an emphasis on energy efficiency to an emphasis on temporal efficiency, respectively.

Domestic sheep, especially lambs, have important qualities that are likely to set them well above most wild prey with respect to their energy value as coyote prey. First, handling costs to coyotes are likely to be low relative to similarly sized wild prey because lambs, and domestic prey in general, tend to lack the anti-predator behavior characteristic of their wild counterparts (see Plate 1). Although lambs are larger than large rodents or lagomorphs, which are thought to represent the optimally sized wild prey of coyotes (Bekoff and Wells 1986, MacCracken and Hansen 1987), it is likely that handling costs, including chase and average success of capture, should be lower for lambs than for

medium-sized wild mammals. Second, search time is likely to be lower than for wild prey because sheep are highly visible from long distances and, on year-round ranches such as HREC, tend to be confined to small pastures, such that their location is predictable. Third, the abundance of domestic sheep in pastures (i.e., a "patch") is usually high enough that the coyote will not deplete the patch by returning repeatedly. Finally, a pair of coyotes can be energetically sustained for 2 d on a single lamb kill (Sacks et al. 1999b), whereas ~10 jackrabbits (*Lepus* spp.) or 20 ground squirrels (*Spermophilus* spp.) would be required to sustain a pair for the same period (Bekoff and Wells 1986). Thus, from a strictly energetic perspective, it seems that breeding coyotes should specialize on lambs.

Coyotes have highly variable litter size thought to be dependent on nutritional condition (Knowlton 1972, Knowlton et al. 1999), which should tend to push coyotes, in particular breeders, toward an energy maximizer foraging strategy relative to many other carnivores (Schoener 1971). Even so, energy intake rate can only translate to increased litter size up to a point, beyond which litter size would not increase. Therefore, costs associated with energy maximizing (e.g., time away from other activities related to survival and reproductive success) should outweigh reproductive benefits beyond some optimal energy efficiency. Breeding coyotes are territorial, which requires that they travel throughout their territories scent-marking, excluding conspecifics, and otherwise maintaining territory integrity. Hence, it is not only the relative energy value of available prey that should determine whether coyotes specialize on one of them, but the absolute availability of prey in general. For this reason, coyote populations are likely to be positioned more or less toward an energy maximizer or time minimizer foraging strategy depending partly on overall prey abundance.

Our study was conducted in a prey-rich, Mediterranean environment during a flush period, potentially reducing the importance of energy efficiency to foraging coyotes. Conversely, coyote density was high (Sacks 1996), which may have increased the time required by breeding coyotes to maintain territories. On the other hand, territories were also small (Sacks 1996), such that movement from one end to the other, when necessary to kill a lamb or defend the territory, required relatively little time. Thus, it was primarily an empirical matter whether coyotes specialized on sheep.

To determine whether breeding coyotes specialized on sheep (adult ewes and lambs) or lambs, we monitored predation rates of breeding pairs on sheep and lambs in territories with different numbers of these available. The prediction of the time minimizer model is that coyotes would not specialize on any prey. The prediction of the energy maximizer model is that coyotes would specialize on the most energetically optimal prey (presumably lambs). It is possible that some other prey was more energetically optimal than sheep. There-



PLATE 1. A pair of coyotes completing a lamb kill while a second lamb looks on. Photograph courtesy of Guy Connolly.

fore, we used contents of coyote feces to additionally investigate coyote consumption of five principal wild prey: brush rabbit (*Sylvilagus bachmani*), dusky-footed woodrat (*Neotoma fuscipes*), black-tailed deer (*Odocoileus hemionus columbianus*), pocket gopher (*Thomomys bottae*), and California vole (*Microtus californicus*). Specifically, we compared consumption of these prey among territories in relation to abundance indexes of these prey to determine if coyotes specialized on any of them. To further elucidate the overall foraging strategy of coyotes, we also compared consumption of these wild prey to abundance of sheep among territories. Finally, to better characterize this relationship with a wild prey of similar body size to sheep, we examined the monthly consumption of deer on vs. off sheep range and compared monthly consumption of deer on the sheep range to sheep kill rate.

METHODS

Study area

We conducted our study during January 1994–May 1996 on and adjacent to the HREC, in the mountains of the Coast Range in Mendocino County, California, USA (39°00' N, 123°05' W). Vegetation occurred in a mosaic of oak woodland, annual grassland, mixed evergreen–deciduous forest, and chaparral (Murphy and Heady 1983). The natural coyote prey base was diverse and included black-tailed deer, two lagomorphs, and numerous rodent species (Neale 1996). The climate was Mediterranean, characterized by a winter wet season and summer dry season. The study was conducted during a flush period, which began 2 yr after a 6-yr drought. The HREC had been used extensively for research on sheep production since 1951 and was grazed

year-round by 900–1500 ewes (Timm 1990). Lambs were present primarily during January–May (lambing period). Sheep were contained in several of 32 fenced pastures ranging from 6 to 260 ha. Most fences were ~1 m high and were (usually) impermeable to sheep but posed little or no obstacle to coyotes, which frequently crawled through holes under or jumped over fences.

Field methods

We used radiotelemetry to delimit coyote territories as described by Sacks et al. (1999b). We quantified abundance (i.e., numbers) of lambs and ewes in each territory on a weekly basis. We documented coyote predation on sheep through daily searches of pastures for dead sheep, field necropsies, and radiotelemetry of coyotes to assign kills to individuals or pairs (Sacks et al. 1999b). We located approximately half of all dead or missing sheep and, based on ratios of found to missing sheep, determined that search success was similar among territories (Sacks 1996). In addition, thorough searches in a subset of pastures indicated that causes of mortality were distributed similarly among found and missing sheep (Neale et al. 1998), suggesting that our estimates of sheep predation were unbiased.

To estimate consumption of prey, we collected recently deposited coyote scats opportunistically throughout the site and every two weeks from 21 500-m transects spread throughout the study area, during June 1994–September 1995. Coyote territories were mutually exclusive and transient individuals avoided territories (Sacks et al. 1999b). Therefore, scats collected in known coyote territories were assumed to have been deposited by residents (Bowen 1981, Andelt 1985), i.e.,

breeders, their pups, and 0–2 pack associates (Sacks 1996). Scats were oven-dried, placed in nylon bags, washed in an automatic washing machine, and then dried in a clothes dryer (Kelly 1991, Neale 1996). Prey remains were identified using a reference collection and hair keys (e.g., Mayer 1952). Most prey were mammals and only mammalian species occurring in $\geq 5\%$ of scats were included in analyses. Several species of mice (*Peromyscus* spp., *Reithrodontomys megalotis*) also occurred in $\geq 5\%$ coyote scats, but because we could not consistently differentiate among these from available remains, they were excluded from analyses.

Data analyses

To determine whether coyotes specialized on sheep (or lambs) during lambing periods, we regressed, among territories, mean sheep kill rate on mean sheep abundance. A significant (positive) slope would indicate that the coyote population was not characterized by sheep specialists, but rather that individuals either preyed opportunistically or exhibited different responses to sheep depending on abundance in the territory (Fig. 1). Lack of a significant regression would support the specialization hypothesis if the mean kill rate was “high.” Sacks (1996) estimated that a breeding pair could be sustained energetically by ≥ 15 sheep/mo, based on how much meat typically was eaten from a kill (similar amount for lambs and ewes).

We performed regression analyses among territories for consumption of each of five principal wild prey species on (1) sheep abundance and (2) suitable habitat of that wild prey as a proxy for prey abundance. We calculated the proportion of each territory composed of “suitable” habitat (cover or open) using a geographic information system (Arcview, version 3.2, ESRI, Redlands, California, USA) to overlay coyote territories on a vegetation layer (Fox et al. 1997; a wildlife habitat map and database for the ORCA [Oregon-California] Klamath Bioregion derived from Landsat imagery, version 1.0a).³ Brush rabbit, woodrat, and black-tailed deer were designated as cover (chaparral/forest/woodland) species, and pocket gopher and vole were designated as open (grassland) species (Jameson and Peeters 1988).

For each wild prey species, we regressed consumption on habitat, sheep, and habitat and sheep together. Statistics for the models with the highest adjusted R^2 values were reported. Because the suitable habitat likely corresponded only approximately to actual prey abundance, we treated it as an ordinal index. Specifically, we ranked the territories with respect to composition of the habitat types and used these ranks in analyses. We transformed numbers of sheep [$\ln(x + 1)$] and proportions of scats composed by each prey [$\arcsin(\sqrt{x})$] within each territory to linearize and normalize data, respectively (Zar 1984). Statistical anal-

³ URL: <http://www.humboldt.edu/~sisi/projects/klamath.htm>

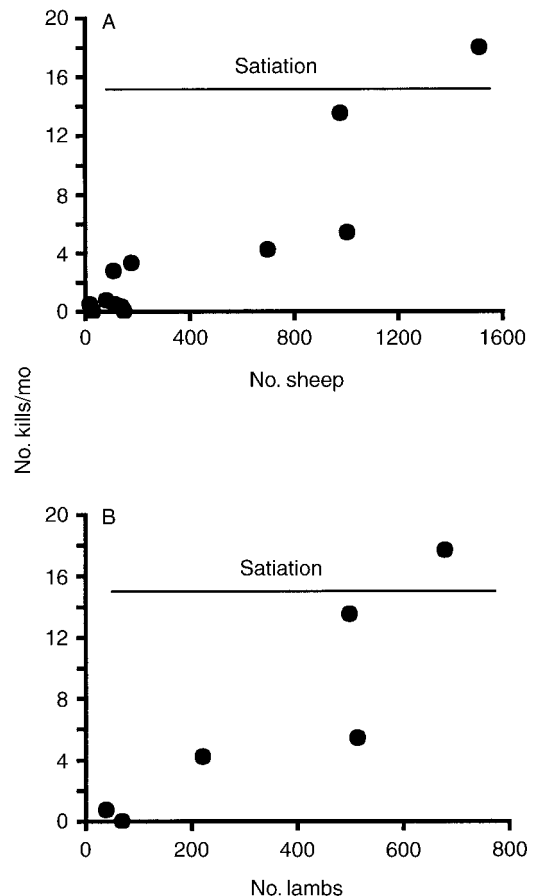


FIG. 2. (A) Sheep (ewes and lambs) kill rate in relation to the abundance of sheep in the territory (means, $n = 12$) and (B) lamb kill rate in relation to the abundance of lambs in the territory (means, $n = 6$) during lambing in 1994, 1995, and 1996 at the Hopland Research and Extension Center (HREC), Mendocino County, California, USA. Satiation lines indicate approximate kill rates necessary for coyotes to meet energy needs solely from freshly killed sheep (assuming one meal per coyote per kill).

yses were performed in SYSTAT (version 5.0, Evanston, Illinois, USA).

RESULTS

During the lambing periods of 1994–1996, 185 coyote-killed sheep, including 158 lambs, were found. These kills were distributed among territories of nine different coyote pairs for 1–2 lambing periods ($n = 12$ pair-years). Coyote kill rates on sheep and lambs increased with their abundance in coyote territories (sheep, adjusted $R^2 = 0.82$, $F_{1,10} = 52.44$, $P < 0.001$; lambs, adjusted $R^2 = 0.76$, $F_{1,4} = 17.11$, $P = 0.014$; Fig. 2).

We analyzed 467 coyote scats collected from five known territories overlapping sheep range and surrounding areas off the sheep range during a 16-mo period of the study. Occurrence in scats of the three cover species (brush rabbit, woodrat, and deer) in-

TABLE 1. Regressions of prey consumption on proportions of territory composed of suitable habitat and abundance of sheep, June 1994–September 1995.

Prey	<i>t</i>		Overall $F_{2,2}$	Adjusted R^2
	Habitat	Sheep		
Brush rabbit‡	7.73**	...	59.77**	0.94
Dusky-footed woodrat	7.12**	...	50.53**	0.93
Black-tailed deer	3.02†	-4.98*	94.78**	0.98
California vole	0.38	0.28	0.64	<0.01
Pocket gopher	-1.67	1.81	1.67	0.25

Note: Regressions were performed with each predictor variable alone and together in a multiple regression; statistics are shown for only the best models.

† $P \leq 0.10$; * $P \leq 0.05$; ** $P \leq 0.01$.

‡ This category probably included a small proportion of juvenile jackrabbit (*Lepus californicus*), which could not be discriminated from the smaller brush rabbits.

creased with increasing proportions of suitable habitat; relationships were less clear for grassland species (pocket gopher and vole; Table 1, Fig. 3). Among wild prey, deer was found at the highest ($n = 4$ territories) or second highest ($n = 1$ territory) frequency in scats (Kruskall-Wallis $\chi^2_4 = 9.96$, $P = 0.04$). When deer was excluded from the analysis, no wild prey ranked consistently among territories with respect to its relative frequency of occurrence in scats (Kruskall-Wallis $\chi^2_3 = 1.18$, $P = 0.76$). Relationships between consumption of wild prey and the (logarithm of) abundance of sheep were significant only for deer; this correlation was negative (Table 1; Fig. 4). Independent variables were not overly intercorrelated (habitat vs. sheep abundance, $r = -0.19$).

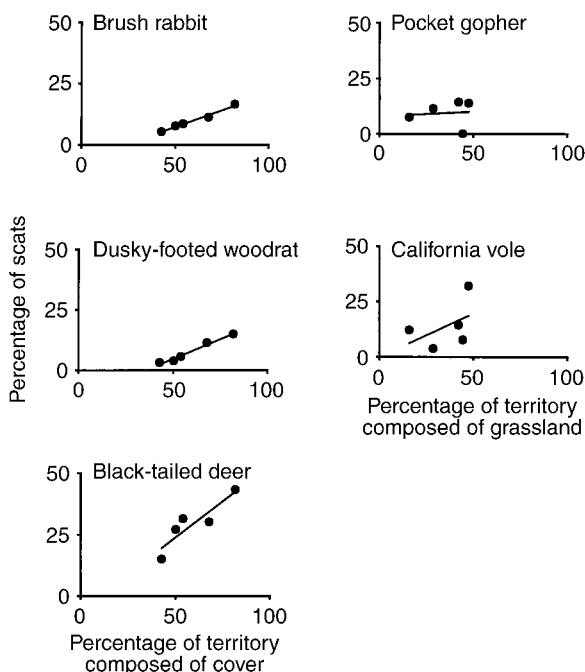


FIG. 3. Relationships between occurrence of wild prey in coyote scats and the proportional amount of suitable habitat for those prey in the territory ($n = 5$), June 1994–September 1995.

Occurrence of deer in coyote scats collected during the lambing period on sheep range was lower than in scats collected off-range during this period (Fig. 5A). The difference between off-range and on-range occurrence of deer in scats was least in early summer, when fawns were present and after most lambs were sold, and during late fall. The occurrence of deer in scats was negatively correlated with the number of sheep kills during the lambing period ($r = -0.99$, $P = 0.001$) but not during the non-lambing period ($r = 0.08$, $P = 0.87$; Fig. 5B).

DISCUSSION

Our findings led us to reject the hypothesis that the breeding coyote population specialized on sheep. Sheep and lambs were killed by breeding coyotes approximately in proportion to abundance of these prey in territories, yet, in every territory, sheep were available in considerable excess of what was killed. Whether the pattern reflected a truly linear relationship or a weakly sigmoid relationship between predation rate and abundance could not be resolved from the data (Fig. 2). In either case, it was clear that coyote pairs with relatively low availability of sheep or lambs did not prey disproportionately more on these prey than did pairs with higher availability.

We also found no evidence that coyotes specialized

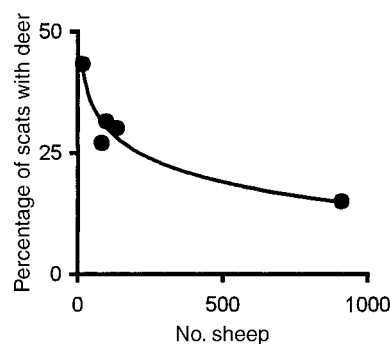


FIG. 4. Occurrence of deer in coyote scats in relation to the mean abundance of sheep in the territory ($n = 5$), June 1994–September 1995.

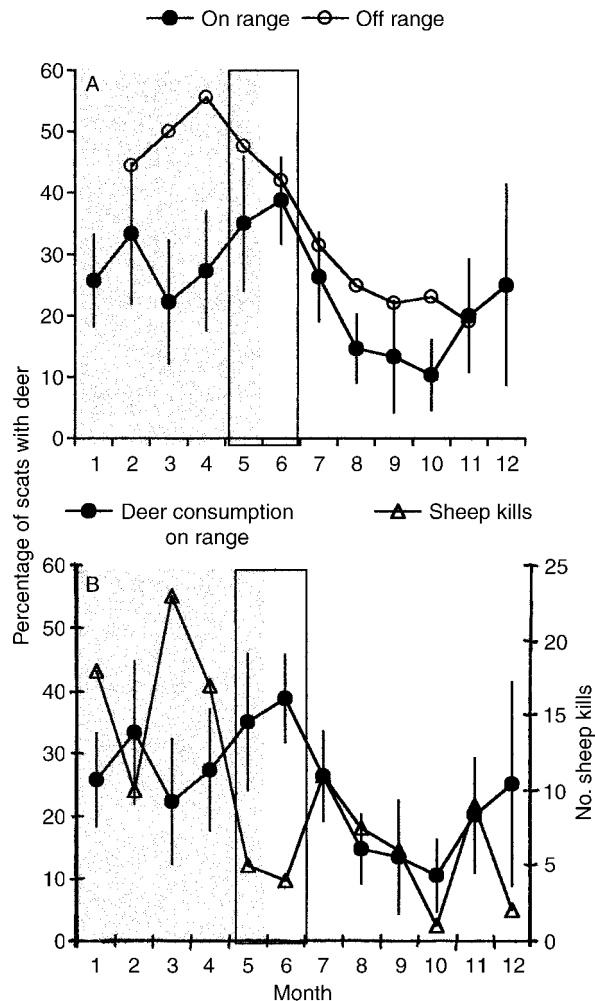


FIG. 5. Monthly occurrence of deer in coyote scats in four territories overlapping sheep pastures (on range; $n = 313$ scats) in relation to (A) occurrence of deer in coyote scats from outside these territories and off the sheep range (off range; $n = 154$) and (B) numbers of sheep kills, June 1994–September 1995. Error bars represent binomial standard errors (± 1 SE). The shaded region indicates lambing, and the boxed area indicates fawning. Scats were pooled and kills averaged for summer months (June–August) of 1994 and 1995. A 3-mo running average was used to display occurrence in off-range scats in (A) due to small sample sizes in some months.

on any other of the five principal wild prey. All wild prey were either consumed in proportion to the amount of suitable habitat in a territory (deer, woodrat, brush rabbit) or there was no clear relationship (pocket gopher, vole). Moreover, with the exception of deer, no wild prey was consumed frequently in all territories. Consumption of deer was probably considerably greater than that of small mammals in all territories given that the index we used, frequency of occurrence, tends to underestimate consumption of large relative to small prey (Weaver 1993). Indeed, based on estimates of biomass consumption for the entire study area, deer (32%)

and sheep (24%) composed considerably greater proportions of the coyote diet than did any small prey, among which the greatest consumption was of woodrat (10%), vole (8%), and lagomorph (6%; Neale and Sacks 2001). Estimated biomass consumption of miscellaneous rodents not included in the present study totaled $<8\%$.

Based on multiple regressions, sheep presence in a territory had no discernable effect on consumption of small mammals but apparently reduced consumption of deer. This relationship between sheep abundance and deer consumption was further supported by the observation that deer were consumed less on sheep range relative to off range during the lambing period (when the more optimally sized sheep were available) but not the non-lambing period and by an inverse relationship between sheep kill rate and deer consumption over time during the lambing period.

That we detected a clear relationship between sheep abundance and deer consumption but not between sheep abundance and consumption of smaller prey could partly have been due to the generally lower consumption of small mammals, which would have weakened our power to detect effects. Further, on our study area, it was breeding coyotes that killed most if not all sheep (Sacks et al. 1999b) and, based on observations elsewhere (Gese and Grothe 1995), these were likely the same individuals that killed deer. Much of the small-mammal consumption, however, was likely due to nonbreeding coyotes, which would not have been directly affected by the presence of sheep. Although nonbreeders commonly scavenge sheep carcasses (Roy and Dorrance 1985, Sacks 1996, Sacks et al. 1999b), sheep consumption was not proportional to sheep abundance in this study (B. N. Sacks, *personal observation*). Unfortunately, we are limited in our interpretations based on scat data because we could not differentiate consumption by breeders from that by nonbreeders, nor could we consistently differentiate scavenging from predation.

Our finding that the coyote population did not specialize on sheep does not imply that no individual breeding coyotes specialized on sheep. Indeed, some coyotes in this study killed similarly high numbers of sheep in months when abundance of sheep was low as when abundance of sheep was high, suggesting that those individuals specialized on sheep (Sacks et al. 1999b). Such a pattern resulted in a type II functional response to changes in numbers of lambs over time in territories with high mean abundance of lambs (B. N. Sacks, *personal observation*), analogous to the specialist curve shown in Fig. 1. Coyotes, like many predators (Murdoch 1969), probably learn, form search images, or otherwise habituate to particular prey such that encounter rates with a prey may influence the ontogeny of prey choice behavior. For example, high exposure to sheep during a sensitive period of development could lead a coyote to develop a search image for sheep and

subsequently become a sheep specialist. This pattern, whereby coyote pairs with high abundances of sheep become sheep specialists but pairs with low abundances of sheep prey opportunistically on sheep, is analogous to a prey-switching response (*sensu* Murdoch 1969) of an individual to changes in relative prey abundances over time.

In summary, the breeding coyote population as a whole did not specialize on sheep, lambs, or any other prey, and clearly killed sheep and lambs in approximate proportion to their abundance in territories. Moreover, deer, the only substantially consumed prey other than sheep, also was consumed in proportion to its abundance in territories. These findings indicate that coyotes did not forage according to predictions of an energy maximizer model. This conclusion seems most apparent when sheep predation and deer consumption are compared. Based on estimates of deer density at HREC (14.6 deer/km²; McCullough 2001), deer abundance on the study area as a whole was 6–7 times lower than that of sheep and 3–4 times lower than lambs alone. Relative to sheep, however, deer were evenly distributed across the landscape such that the territories with the highest abundances of sheep likely had >10:1 ratios of sheep to deer, whereas territories with the lowest abundances of sheep probably had sheep:deer ratios ≤1:1. Within territories, sheep also were more clustered than deer. If we assume that sheep, especially lambs, were a more energetically optimal prey than deer (which were all large during lambing), then the observation that lambs were not taken in high numbers in territories where lamb:deer ratios were close to 1:1 clearly indicates that factors other than energy efficiency determined coyote prey selection. Possibly, relatively uniform spatial dispersion was more important than high abundance in a territory in determining availability of prey to coyotes. Such would be the case if coyotes foraged according to a time minimizer strategy, whereby they moved throughout their territories primarily for reasons unassociated with foraging, such as territory maintenance, and took prey opportunistically, *i.e.*, as they encountered them. Additionally, if coyotes perceived risk in killing sheep, for example, due to increased probability of being trapped in the vicinity of sheep, this also could partly explain their lack of specialization on sheep. Nevertheless, the cumulative findings of this study support the hypothesis that coyotes tended toward a time minimizer strategy and clearly refute the hypothesis that coyotes foraged primarily as energy maximizers.

A management implication of these findings is that predation on sheep in our study area could be minimized by concentrating sheep in as small an area as possible. Our findings likely are applicable to other similarly prey-rich environments. Coyote populations in more food-limited environments, however, might be more likely to forage as energy maximizers and, hence, to specialize on domestic ungulates, regardless of spa-

tial distribution. For example, in a Chihuahuan desert region of New Mexico, where lagomorphs represented the staple prey of coyotes, 12 of 34 goat kids experimentally introduced were killed by coyotes almost immediately (<3 wk), even though the ranges of goat flocks overlapped only small parts of the coyote territories in which kid remains were found (Windberg et al. 1997). Studies similar to ours in different environments would be valuable in an effort to gain a more complete understanding of coyote foraging strategies.

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