

Coyote prey selection and community stability during a decline in food supply

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The foraging behavior of predators can have a large influence on community dynamics and has been shown to increase stability in some cases and decrease stability in others. I studied the foraging behavior of coyotes (*Canis latrans*) in the Alaska Range during the peak and decline of a snowshoe hare (*Lepus americanus*) population cycle (1999–2002). Coyote diet was compared with prey availability to test for changes in prey selection and to examine the effect of coyote predation on the vertebrate prey community. Coyotes responded to the hare decline by increasing selection for hares and porcupines, whereas selection for voles, ground squirrels and Dall sheep did not change. Although the study area was characterized by considerable habitat heterogeneity, coyotes utilized the area as a fine-grained environment. Coyote foraging behavior was driven primarily by changes in snowshoe hare abundance, and their sensitivity to change in alternative prey density was low. Predation by coyotes may therefore decrease the stability of alternative prey populations rather than dampening fluctuations. In order for predation to enhance the stability of prey populations, I hypothesize that prey profitability must be determined primarily by abundance.

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The effect of predation on community stability has long been disputed. Theoretical models and empirical studies have shown that predation does not have the same effect in all communities. Predation can increase the amplitudes of fluctuations in prey abundance (van Baalen et al. 2001), dampen fluctuations (Fryxell and Lundberg 1994), increase the probability of prey extinctions (Holt 1977), or decrease the probability of extinctions (Krivan and Eisner 2003). Thus, the relevant question is not whether predation increases or decreases community stability, but rather, under what conditions is predation stabilizing or destabilizing?

A distinction is commonly made between specialist and generalist predators, and it has been hypothesized that predation by generalists leads to stability whereas predation by specialists leads to instability. For example, Hanski et al. (1991) propose that specialist predators in

northern Fennoscandia drive large-amplitude population cycles in voles, whereas generalist predators in southern Fennoscandia dampen prey fluctuations. Likewise, the predator-mediated coexistence hypothesis states that frequency-dependent predation by “keystone” generalist predators can lead to coexistence among competing prey because the dominant competitor is prevented from excluding inferior competitors (Paine 1966, Caswell 1978, Henke and Bryant 1999).

Although several cases of keystone predation have been documented (most famously, *Pisaster* in intertidal communities; Paine 1966), predation by generalists can also reduce the likelihood of prey coexistence by inducing apparent competition among prey that do not compete directly (Holt 1977). When the primary prey supports a dense predator population that also feeds on secondary prey, predation can reduce secondary prey

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populations or drive them extinct (Holt and Lawton 1994, Bonsall and Hassell 1997). Thus, generalist predators have been shown to increase prey diversity and stability in some cases and reduce diversity and stability in others.

Prey switching is a foraging behavior commonly associated with generalist predators that can affect community stability (Murdoch and Oaten 1975, Oaten and Murdoch 1975, Abrams 1999, van Baalen et al. 2001). This behavior is a specific pattern of change in resource selection in which a predator's selection for a prey species increases when that species is abundant and decreases when it is scarce (Murdoch 1969). Theoretically, switching among alternative prey can increase the stability of a predator-prey system by dampening fluctuations in populations and reducing the effects of apparent competition (Oaten and Murdoch 1975, Holt 1977, Erlinge et al. 1984, Abrams and Matsuda 1996). Prey switching has been documented in field and laboratory studies (Lawton et al. 1974, Murdoch et al. 1975, Akre and Johnson 1979, Hughes and Croy 1993, O'Donoghue et al. 1998a), but studies have also documented cases in which generalist predators did not switch prey (Akre and Johnson 1979, Corbett and Newsome 1987, Jaksic et al. 1992, Dale et al. 1994, White et al. 1996, O'Donoghue et al. 1998a). Murdoch (1969) found that predatory snails would not switch prey if their preference for one prey item was strong, but they would switch if preference was weak. Predators often have strong preferences for particular prey types, and in these cases the absolute abundance of the preferred prey can determine prey choice rather than relative prey abundance (Davies 1977, Windberg and Mitchell 1990, Leckie et al. 1998). When prey-switching occurs in response to absolute primary prey abundance, switching behavior can be destabilizing because predation on alternative prey is not density dependent (Norbury 2001).

Predators may have strong preferences for the most profitable prey type, and optimal foraging models predict that predators should always include the most profitable prey item in their diet regardless of its abundance (Charnov 1976). Less profitable prey should be added in decreasing order of profitability when the abundance of the most profitable prey falls below a threshold (Charnov 1976, Krebs 1978). Optimal foraging by predators should destabilize dynamics in most situations (Kriwan and Sikder 1999, Oksanen et al. 2001, van Baalen et al. 2001, Bolker et al. 2003). However, if alternative prey occur in different habitats than primary prey, adaptive foraging may lead to habitat switching by the predator, and this behavior can increase stability (Holt 1984, Oksanen et al. 2001, Schmidt 2004). Most studies of foraging behavior and stability have been theoretical, and relatively few studies have examined these theories empirically. In this paper, I evaluate the

foraging behavior of coyotes (*Canis latrans*) in an area with considerable habitat heterogeneity and examine the consequences of their behavior for the vertebrate prey community.

Coyotes are known to consume a wide variety of prey items and have long been regarded as prototypical generalists (Young and Jackson 1951, Bekoff 1977). However, several studies have shown that coyotes can be selective predators, and changes in resource availability can strongly affect their patterns of resource use (Windberg and Mitchell 1990, O'Donoghue et al. 1998b). In northern Canada and Alaska, snowshoe hares (*Lepus americanus*) are the primary prey of coyotes (Thurber et al. 1992, O'Donoghue 1997). Snowshoe hare populations fluctuate 10–25-fold with cyclic peaks every 8–11 years (Hodges 2000). A 10-year study in the Yukon found that coyotes did not switch from snowshoe hares to alternative prey when hares declined (O'Donoghue et al. 1998a).

The goals of this study were to examine the behavioral response of coyotes to a steep decline in snowshoe hare abundance in the central Alaska Range and to assess the impact of changes in coyote foraging behavior on alternative prey, such as Dall sheep (*Ovis dalli*). A previous study of Dall sheep mortality in this area found that coyotes were the main predators of lambs (Scotton 1998). The study site contained a patchy mixture of northern boreal forest, subalpine shrub and high-elevation alpine tundra habitats (Fig. 1). This tapestry of habitat types resulted in relatively high prey diversity and abundance, and combined with the natural

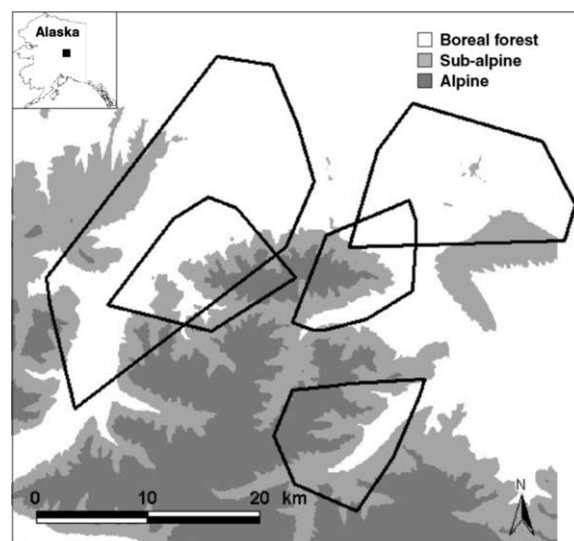


Fig. 1. Central Alaska Range study area (63°57'N, 147°18'W) showing the three major habitat classifications (boreal forest, 600–1000 m; subalpine shrub, 1000–1400 m; alpine meadow, 1400–2100 m) and home ranges of five radiocollared coyote pairs (polygons). Each home range is the 100% minimum convex polygon enclosing all locations of each pair from 1999–2002.

experiment of rapidly declining hare density, provided an ideal setting to empirically test foraging theories. I tested two alternative hypotheses:

- H₁: Coyote selection for hares would be high regardless of hare density and alternative prey would be added to the diet when hare density reached a low threshold. Absolute hare density would be the best predictor of coyote diet.
- H₂: Coyote selection for hares would decrease as hare abundance declined because coyotes would leave hare habitat to forage for alternative prey such as Dall sheep or voles. Relative prey density would be the best predictor of coyote diet.

Study area

This study was conducted from May 1999 to July 2002 in the central Alaska Range (Fig. 1; 63°57' N, 147°18' W). The area encompassed 1000 km² of mountains and foothills on the northern edge of the Alaska Range, approximately 80 km south of Fairbanks. Elevation ranged from 600–2100 m. Potential coyote prey species included snowshoe hare (*Lepus americanus*), Dall sheep (*Ovis dalli*), moose (*Alces alces*), caribou (*Rangifer tarandus*), ground squirrel (*Spermophilus parryi*), voles (*Clethrionomys rutilus*, *Microtus* spp.), red squirrel (*Tamiasciurus hudsonicus*), porcupine (*Erethizon dorsatum*), ptarmigan (*Lagopus* spp.), and grouse (*Dendragapus canadensis* and *Tympanuchus phasianellus*). Other major predators in the area included grey wolves (*Canis lupus*), red fox (*Vulpes vulpes*), pine marten (*Martes americana*), wolverine (*Gulo gulo*), lynx (*Lynx canadensis*), grizzly bear (*Ursus arctos*), and black bear (*Ursus americanus*). Snowshoe hare habitat consisted of willow (*Salix* spp.) and alder (*Alnus* spp.) thickets and closed-canopy white spruce (*Picea glauca*) forests, and these cover types made up approximately 43% of the study area (boreal forest, Fig. 1). Moose, red squirrel, grouse, and porcupine also occurred primarily in these lower-elevation cover types. Hare habitat bordered Dall sheep habitat, which consisted of alpine meadows and bare rock at higher elevations and some subalpine shrub areas (1000–2600 m; Fig. 1). Ground squirrels and ptarmigan occurred primarily in these higher elevation habitats, and voles occurred in grassy meadows that were distributed throughout the study area. The home ranges of most radiocollared coyotes included both high and low elevation habitats (Fig. 1).

Methods

Estimating prey abundance

Small mammals

Snowshoe hare, ground squirrel and vole densities were estimated using a combination of mark–recapture estimates and population indices. Procedures for hand-

ling live animals were conducted in accordance with Animal Care protocols approved by the University of British Columbia and permits were granted by the Alaska Department of Fish and Game. A 9.4 ha live-trapping grid was established in a white spruce forest to obtain estimates of hare density. Ground squirrel density was estimated on two 1.3 ha live-trapping grids, one in the subalpine and one in the alpine. A 0.36 ha live-trapping grid was established in a shrub/meadow habitat to obtain estimates of vole density. Capture sessions occurred during 3–5 consecutive days, and captured animals were marked with numbered ear tags (National Band and Tag Co., Newport, KY). The program CAPTURE (Otis et al. 1978) was used to calculate mark–recapture estimates using the jackknife heterogeneity estimator (Boulanger and Krebs 1996). The snowshoe hare trapping grid was surrounded by open habitat inhospitable to hares, so the mark–recapture estimate was converted to a density estimate by dividing the number of hares by the area of the trapping grid. For ground squirrel and vole density estimates, a buffer strip the width of the average movement distance between recaptures was added to the area of the grid (squirrels = 46.8 m, voles = 18.7 m).

The snowshoe hare trapping grid was not established in preferred hare habitat, because the grid was too large to fit in the narrow, discontinuous strips of willow and alder that are preferred habitat in this area. As a result, a mark–recapture estimate could only be obtained in 1999, when hares were most abundant. Hare fecal pellets were counted on 126 plots within the trapping grid to calibrate pellet counts with the mark–recapture estimate (Krebs et al. 2001, Murray et al. 2002). Additional pellet plot grids in three habitat types (spruce, alder, and willow) were established throughout the study area ($n = 11$). At least 50 permanent plots spaced 15 m apart were established on each grid. Circular plots of 25-cm radius (0.20 m²) were used on grids with high pellet density, and plots of 50-cm radius (0.79 m²) were used on grids with low pellet density. Plots were counted and cleared once per year (for details of the pellet count protocols see Prugh and Krebs 2004). Pellet counts are an index of hare abundance during the previous year, so there is a lag between changes in hare abundance and changes in pellet counts. To correct for this, I averaged the pellet counts from time t and time $t+1$ when estimating hare abundance at time t .

Tracking boards were used to obtain ground squirrel population indices at four sites in the alpine (Hubbs et al. 2000). Tracking board grids were 30 × 300 m, and every ground squirrel burrow within this area was flagged. Tile samples (5 × 7 cm) were rubbed with paraffin-based oil, dipped in unscented talcum powder, and secured in the burrow entrance with a nail. Tiles were placed in all burrows and retrieved nine hours later. The number of boards with ground squirrel tracks was

used as the index of abundance. Vole population indices were obtained on three live-trapping grids in shrub and meadow habitats of the same design as the vole mark-recapture grid. The number of voles caught during one trap night was used as a minimum-number-alive index. Ground squirrel and vole indices were also conducted on the mark-recapture grids, and the 3-year average calibrations were used to estimate densities on the index grids.

Dall sheep

Annual estimates of Dall sheep abundance were obtained by aerial surveys in June 1999–2001 from a Robinson R22 helicopter. Lambs, ewes, rams, and yearlings were counted in separate categories throughout the study area. Surveys were conducted using the same pilot and observer each year, in similar weather conditions and at the same time of year.

Carriion

Wolf and hunter-killed moose, caribou, and Dall sheep carcasses were commonly scavenged by coyotes. The number of hunter-killed ungulates in the study area was calculated from harvest records at the Alaska Department of Fish and Game (ADF&G), and the number of wolf-killed ungulates was determined from a wolf kill rate study conducted by ADF&G in the study area during winters 1998 and 2000. Carcass density was similar in both years, so I used the average carcass density for the three years of this study. The kill rate in summer months was assumed to be half the rate of winter kills due to changes in wolf social structure and diet (M. McNay, ADF&G, pers. comm.).

Porcupine

An estimate of porcupine abundance was not obtained in the study area because they were rarely seen (four sightings in three years) and not considered to be an important prey item at the outset of the study. Based on other studies of porcupines and the scarcity of sign in our area, we assumed that porcupine density remained constant and low (0.7 ha^{-1}) for the duration of this study (Sweitzer 1996, Zimmerling 2001).

Biomass calculations

Biomass estimates of hares, ground squirrels, and voles per hectare were calculated by multiplying the average weight of live-trapped animals by the respective density estimates. For Dall sheep lambs, the biomass calculation was based on a model incorporating birth rates, mortality rates, and growth rates each year (data from ADF&G and Shackleton et al. 1999), and the yearly average biomass was used. Adult Dall sheep were not

included in the biomass calculation, because coyotes rarely killed adult sheep in this area (Arthur 2003). Carrion biomass was estimated by monitoring fresh wolf-killed carcasses during winter months to estimate the proportion left after abandonment by wolves. For hunter-killed ungulates, 30% of the biomass was assumed to be available to scavengers, based on the amount of meat that hunters were legally required to remove from harvested animals (Alaska Department of Fish and Game 2003). Wolf and hunter-killed ungulates were separated into species, sex, and age categories and multiplied by the appropriate biomass based on ADF&G data.

To facilitate comparison of relative prey biomass, a GIS habitat map was used to quantify available habitat in the study area for hares, ground squirrels, voles, and porcupines based on 24 land cover classifications (Bureau of Land Management 2002). The habitat-specific density estimates for each prey type were multiplied by the hectares of available habitat to provide an estimate of total prey biomass in the study area. Estimates of lamb and carrion biomass were calculated based on counts in the entire study area, so these were not adjusted for habitat.

Coyote diet

Coyote scats were collected to examine coyote diet during summer (May–August) and winter (January–March) 1999–2002. Diet was also examined during winters 2001 and 2002 by recording kills, caches, and scavenging events while following coyote tracks in snow. Diets constructed from both methods were remarkably similar (Prugh 2004), indicating that scats provided a robust measure of coyote diet patterns. Scats were collected opportunistically in summer as we traveled in the study area on foot, and they were collected on snowmobile trails and by backtracking coyotes in winter. Scats were autoclaved to kill *Echinococcus* eggs. Sterile samples were washed in nylon mesh bags using a clothes washing machine on gentle cycle, and samples were air-dried before analysis. Dried scats were carefully examined and all food items present were recorded. The relative amount of each item in the scat was estimated on a scale of 1–5, with 1 = trace amount ($<2\%$), 2 = 2–25%, 3 = 26–50%, 4 = 51–75%, and 5 = 76–100% of scat contents. Hairs, teeth, and claws were compared to reference specimens and guide books (Moore et al. 1974) for identification. Hair medulla patterns were examined under a microscope for identification, and scale impressions were made for all moose and caribou hairs, as well as other hairs that were difficult to identify. Occurrences of moose and caribou in scats were assumed to be the result of scavenging and categorized as carrion, because studies of these species in

this area did not find coyotes to be a significant source of mortality (Boertje et al. 1996). Diet from scats is reported as % weighted occurrence:

$$\% \text{ weighted occurrence}_{\text{prey } i} = \frac{\sum_s X_{is} Y_{is}}{\sum_i XY}$$

where X_{is} = occurrence of prey i in scat s and Y_{is} = relative amount of prey i in scat s (weighting value), divided by the total weighted occurrences of all prey items in the diet. Items with a weighting value of “1” (trace amount) were excluded from analyses. When annual diet is reported, summer and winter scats were pooled (May–August and January–March). I refer to summer 1999/winter 2000 as year 1, summer 2000/winter 2001 as year 2, and summer 2001/winter 2002 as year 3.

Data analysis

Repeated measures analysis of variance was used to test for changes in snowshoe hare, ground squirrel, and vole abundance among years. Hare data were log transformed to meet the assumptions of ANOVA. Diet diversity was calculated using Simpson’s index of diversity on a random subsample of 72 scats each season (Krebs 1999, p. 443), and linear regression was used to examine the effect of hare abundance on diet diversity.

To test for prey switching, the selection ratio for each prey item (% weighted occurrence in diet/relative biomass in study area) was compared among years using Bonferroni adjusted chi-squared tests (after Manly et al. 2002, pp. 57–58). After Bonferroni adjustment, significance of pairwise comparisons were tested at $\alpha = 0.017$ to maintain an overall α of 0.05 over all three comparisons. If the selection ratio for a prey item was low when the prey was scarce and increased when the prey was abundant, I considered this evidence of prey switching. Selection ratios were only used as “ballpark” estimates of predator preference in this study, because occurrence of items in scats may not be directly proportional to biomass ingested for each prey type. Small prey tend to be overestimated and large prey tend to be underestimated by scat analysis due differences in the ratio of indigestible (hair and bone) to digestible (muscle and organ) material (Johnson and Hansen 1979). This problem affects only the absolute value of the selection ratio, however, and changes in selection ratios over time should accurately reflect changes in coyote selection for prey. It should also be noted that selection ratios can be sensitive to the prey items chosen for analysis (Manly et al. 2002). Reanalysis of this dataset with various combinations of species indicated the selection ratios reported here are robust.

Regression analyses were used to examine the relationship between available prey biomass and coyote diet, using both relative and absolute measures of prey biomass and occurrences in coyote scats. For regression analyses, $\alpha = 0.05$. Analyses were conducted using JMP-IN 4.0 (SAS Institute) and Excel (Microsoft Inc.).

Results

Prey abundance

The abundance of snowshoe hares declined nearly 6-fold from 1999–2001 (Fig. 2a, $F_{1,8} = 68.8$, $P < 0.0001$). Hare biomass made up 68% of total prey biomass in 1999 but only 20% in 2001 (Fig. 3). The hare decline resulted in an overall decline in prey biomass from 1999–2001 (Fig. 2e), although this decline in prey abundance was partially mitigated by the vole irruption in 2001 (Fig. 2c; $F_{1,3} = 9.22$, $P = 0.056$). By 2001, voles represented 61% of available prey biomass (Fig. 3). Ground squirrel abundance was moderate and stable across all years ($F_{1,2} = 4.81$, $P = 0.16$), and the high variance of these estimates indicates that squirrel distribution was patchy (Fig. 2b). Dall sheep lamb biomass declined 50% between 1999 and 2000 and remained low in 2001 (Fig. 2d). Lamb biomass represented only 1% of total prey biomass each year (Fig. 3). After abandonment by wolves, 14.6% of carcass biomass was available to scavengers on average ($n = 8$, 95% CI $\pm 13.46\%$).

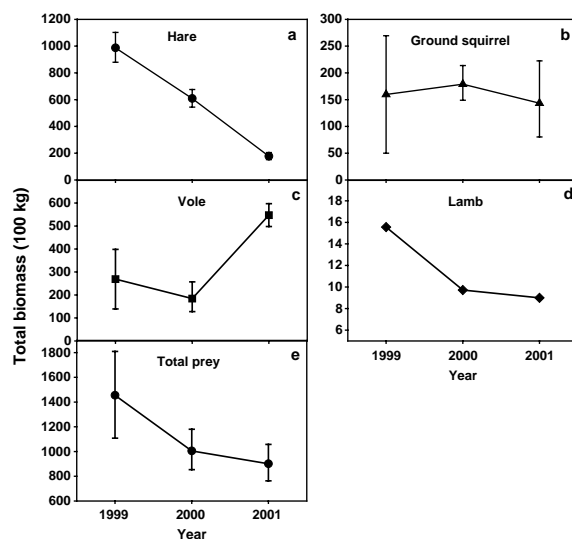


Fig. 2. Annual estimates of (a) hare, (b) ground squirrel, (c) vole, (d) lamb, and (e) total prey biomass in the Alaska Range, 1999–2001. Estimates were adjusted for habitat coverage and represent average total biomass in the 1000 km² study area. Error bars represent 90% confidence intervals of bootstrapped means. Lamb estimates (d) were from total counts. Carcass and porcupine estimates were included in total prey biomass calculations (e).

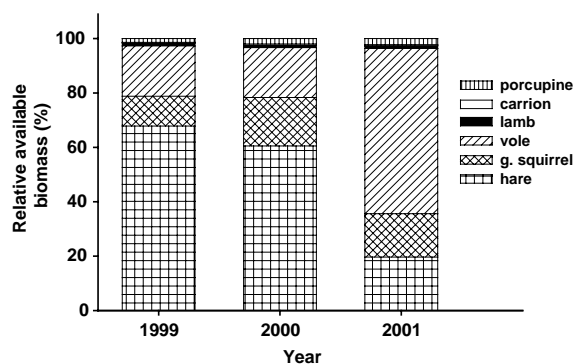


Fig. 3. Relative available biomass of six prey species monitored in the Alaska Range, 1999–2001. Carrion biomass was too negligible (0.3–0.4%) to be visible in this graph.

Approximately 85% of the carrion provided by wolves and hunters was moose. Hunters provided twice as much carrion as wolves but only during the fall hunting season, whereas wolf kills were available year-round. Combined hunter and wolf carrion represented only 0.3–0.4% of total available prey biomass (Fig. 3). Based on an assumed density of 0.7 porcupines per hectare, porcupines represented 1.4–2.2% of the total prey biomass (Fig. 3).

Coyote diet

A total of 1590 coyote scats were collected from 1999–2002. Snowshoe hare was the most prevalent item in coyote scats during years 1 and 2, but carrion surpassed hares as the top prey in year 3 (Fig. 4). Occurrences of hare decreased in the diet as hare abundance declined, whereas carrion, porcupine, and vole occurrences increased, and ground squirrels, Dall sheep, and other items (mainly birds and vegetation)

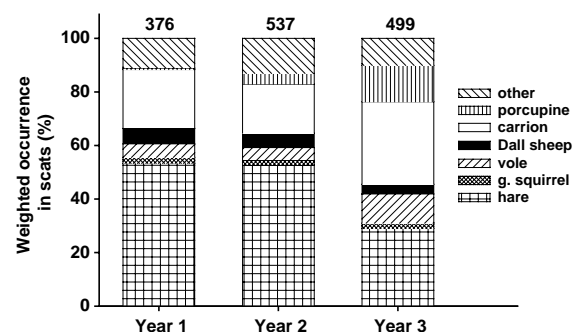


Fig. 4. Relative occurrence of prey items in coyote scats (weighted by the approximate volume of items in each scat) collected in the Alaska Range from 1999–2002. Sample sizes (n scats) are shown above bars. The “other” diet category included mainly birds and vegetation. Year 1 = summer 1999/winter 2000, year 2 = summer 2000/winter 2001, and year 3 = summer 2001/winter 2002.

remained unchanged in the diet (Fig. 4). The proportion of porcupine in the diet increased from 0.53% in year 1 to 13.6% in year 3, and voles increased from 5.0% in year 1 to 10.9% in year 3 (Fig. 4). The diversity of prey items in coyote scats was inversely related to snowshoe hare abundance (Fig. 5, $R^2 = 0.85$, $F_{1,5} = 22.5$, $P = 0.009$). Diet diversity showed no seasonal trends: diversity was slightly higher in summer than winter in year 3 but was slightly lower in years 1 and 2. Thus, hare abundance had a stronger influence on coyote diet breadth than seasonal changes.

Prey preference and switching

Selection ratios were calculated for each prey type each year to test for prey switching. There was no significant change in the selection ratio for hares between years 1 and 2, but coyote selection for hares increased significantly between years 2 and 3 (Table 1, $P < 0.001$). Although the percent occurrence of hares in the diet decreased by 23.8% between years 2 and 3, the availability of hares decreased by 40.8%. Thus, coyote selection for hares actually increased as hares declined.

Voies were the most abundant prey by year 3, but the selection ratio for voles did not increase (Table 1). Carrion was the most preferred prey, because proportional occurrence in the diet was much higher than proportional availability each year (Table 1). Coyote selection for carrion decreased between years 1 and 2 ($\chi^2_1 = 16.10$, $P < 0.001$) and then increased between years 2 and 3 ($\chi^2_1 = 6.90$, $P = 0.009$). Selection for ground squirrels and Dall sheep did not change significantly among years. The selection ratio for porcupines increased significantly each year, which was evidence of prey switching (Table 1, $P < 0.001$).

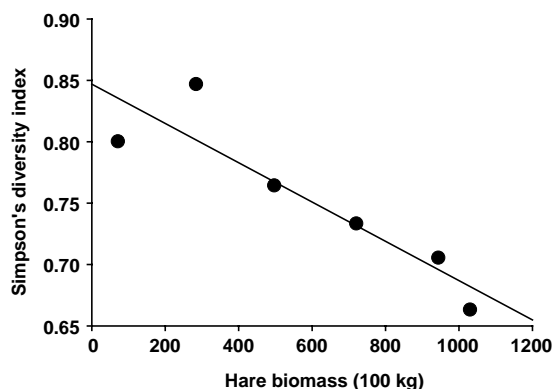


Fig. 5. Relationship between coyote diet diversity and snowshoe hare biomass in the Alaska Range, 1999–2002. Each datapoint represents the Simpson's diversity index for a random subsample of scats ($n = 72$) from each season ($n = 6$), plotted against the corresponding snowshoe hare biomass estimate.

Table 1. Annual estimates of the selection ratios (relative occurrence in scats/relative available biomass) of coyotes for six prey types in the Alaska Range, 1999–2002. Results from χ^2 tests of differences between selection ratios among years are reported. After Bonferroni adjustment, the critical χ^2 value is 5.99. Statistically significant differences ($P < 0.0167$) are in bold.

	Selection ratios			Manly's α			χ^2 values		
	1999	2000	2001	1999	2000	2001	1999 vs 2000	2000 vs 2001	1999 vs 2001
Hare	0.88	1.00	1.62	0.008	0.015	0.018	5.48	30.13	42.42
Squirrel	0.23	0.11	0.15	0.002	0.002	0.002	2.40	0.73	0.85
Vole	0.31	0.30	0.19	0.003	0.004	0.002	0.01	3.57	2.91
Lamb	6.04	6.39	4.88	0.058	0.096	0.054	0.05	1.10	0.58
Porcupine	0.43	2.30	8.28	0.004	0.034	0.092	12.08	43.79	88.74
Carrion	96.19	56.64	74.69	0.924	0.849	0.832	16.10	6.90	4.64
N scats	376	537	499						

Predicting coyote diet

Snowshoe hare biomass was a good predictor of the percent occurrence of hare, carrion, vole, and porcupine in coyote scats (Fig. 6). Absolute hare biomass explained more of the variation in prey occurrence than relative hare biomass (Table 2). As hare biomass increased, occurrence of hare in scats increased (Fig. 6a; $R^2 = 0.73$, $F_{1,5} = 10.99$, $P = 0.03$), occurrence of carrion decreased (Fig. 6b; $R^2 = 0.70$, $F_{1,5} = 9.36$, $P = 0.038$), occurrence of porcupine decreased (Fig. 6c; $R^2 = 0.94$, $F_{1,5} = 63.16$, $P = 0.001$), and occurrence of voles decreased (Fig. 6d; $R^2 = 0.92$, $F_{1,5} = 47.39$, $P = 0.002$).

Occurrences of carrion, porcupine and vole in coyote scats were better predicted by hare biomass than by any other prey biomass (including their own), but Dall sheep occurrence in scats could not be predicted by hare biomass (Table 2; $R^2 = 0.06$, $F_{1,5} = 0.24$, $P = 0.65$) or any other prey biomass (including sheep). Vole biomass was also a good predictor of vole occurrence in the diet (linear function; $R^2 = 0.80$, $F_{1,5} = 16.2$, $P = 0.016$), but this may have been an artifact of the negative correlation between vole and hare biomass ($R = -0.81$, $P = 0.05$).

Discussion

Snowshoe hares were the primary prey of coyotes in the Alaska Range, a finding in agreement with previous studies of northern coyotes (Thurber et al. 1992, O'Donoghue et al. 1998b). Coyote selection for hares did not decrease when hare abundance declined, in fact, their selection for hares increased, and the absolute density of hares was the best predictor of coyote diet composition. These findings support my first hypothesis (H_1), which was based on predictions of optimal foraging theory when predators forage in a fine-grained environment. My second hypothesis (H_2), which predicted that selection for hares would decline due to habitat switching by coyotes foraging in a coarse-grained environment, was not supported. The alternative prey types that coyotes relied on most heavily when hare abundance was low (carrion and porcupine) occurred in the same habitat as hares, so coyotes were able to include these items in their diet without switching habitats. Indeed, there were no significant changes in elevation or habitat usage of radiocollared coyotes during the study (unpubl.). Additionally, what appeared to be a

Fig. 6. The relationship between prey occurrence in coyote scats and snowshoe hare biomass in the Alaska Range, 1999–2002. Percent of coyote scats containing (a) snowshoe hare, (b) moose or caribou carrion, (c) vole, and (d) porcupine are plotted against the corresponding snowshoe hare biomass estimate for each season ($n = 6$ seasons). Dashed line (b) is the linear regression excluding the outlier ($n = 5$). Sample sizes of scats for each estimate vary from 72–407. Regression equations, R^2 values, and P -values of analyses are reported in Table 3 (absolute hare biomass).

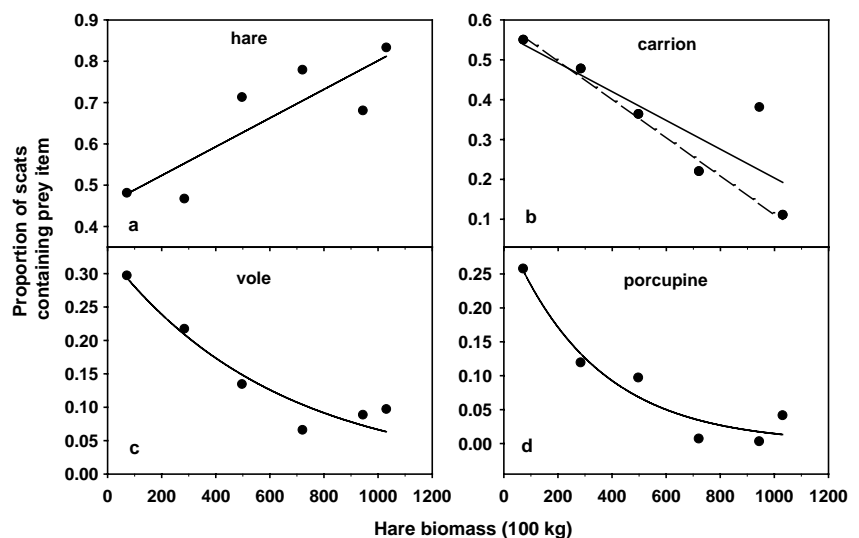


Table 2. Regression analyses of the percent occurrence of five prey species in coyote scats versus absolute hare biomass and relative hare biomass. N=6 seasonal datapoints for each regression, except for carrion (no outlier) n=5. A linear function was used to predict occurrence of hares, carrion, and lamb in the diet, and an exponential decay function was used for vole and porcupine. Significant relationships are in bold. Figure 5 shows graphs of the regressions with absolute hare biomass.

Prey in diet	Absolute hare biomass			Relative hare biomass		
	Equation	R ²	P-value	Equation	R ²	P-value
Hare	$y = 0.454 + 0.0000035x$	0.73	0.030	$y = 30.0 + 0.504x$	0.62	0.063
Vole	$y = 0.329 \times \exp(-0.002x)$	0.92	0.002	$y = 14.7 \times \exp(-0.017x)$	0.86	0.008
Porcupine	$y = 0.318 \times \exp(-0.003x)$	0.94	0.001	$y = 30.9 \times \exp(-0.059x)$	0.82	0.014
Carrion	$y = 0.56 - 0.0004x$	0.70	0.038	$y = 32.72 - 0.2055x$	0.29	0.335
(no outlier)	$y = 0.595 - 0.0000048x$	0.99	0.001	$y = 3625 - 0.334x$	0.56	0.143
Lamb	$y = 0.084 - 0.0000002x$	0.06	0.650	$y = 4.31 + 0.019x$	0.03	0.753

patchy, heterogeneous habitat landscape in my study area may have been utilized as a fine-grained environment by coyotes. The home ranges of most radiocollared coyotes in this area included all major habitat types (Fig. 1) and coyotes moved among habitat patches on a daily basis during all years (ADF&G, unpubl.). Although habitat patchiness is often shown to increase the stability of predator-prey interactions in theoretical analyses (Holt 1984, Oksanen et al. 2001, Schmidt 2004), few studies have demonstrated this effect in the field (Schmitt 1987, Seip 1992).

Profitability and thresholds

As predicted by H_1 , alternative prey were added to the diet of coyotes as hare density declined, but not in the pattern predicted by optimal foraging theory (Stephens and Krebs 1986). There was no evidence of a threshold hare density that affected inclusion of alternative prey in the diet. Alternative prey were consumed during peak hare abundance, and the addition of new prey items to the diet was linear during the hare decline (Fig. 5). Partial preferences and a gradual shift in diet, which is considered "semi-optimal" (Oksanen et al. 2001), is often observed in field studies and may occur due to imperfect knowledge, sampling, or nutritional constraints (Emlen and Emlen 1975, Belovsky 1981, Berec 2000). It is also possible that hare density never exceeded the level beyond which it would become advantageous for coyotes to ignore all other prey items encountered.

Use of the term "profitable" may lead to some confusion, because this term may or may not account for prey density (Norberg 1977, Hughes and Croy 1993). Because optimal foraging theory predicts a profitable item should be consumed regardless of its density, this can be thought of as "intrinsic profitability." Many factors will influence the intrinsic profitability of a prey item, such as size, vulnerability, and nutritional content, and the profitability of an item to a predator can increase with predator experience (Werner and Hall 1974, Werner et al. 1981, Sutherland 1982, Croy and Hughes 1991). Intrinsic profitability therefore does not include search

time, which will be strongly affected by prey density. I will use the term "net profitability" when including search time in the evaluation of energy expenditure by the foraging predator. For a prey species that has a high intrinsic profitability ranking but is rare, it may be advantageous for the predator to attack the prey if it is encountered opportunistically, but it should rarely encounter this prey during random searches. If a specialized hunting technique is required to capture an intrinsically profitable prey item, it may not be advantageous to specifically search for it if that prey is rare.

Selection for alternative prey

In contrast to a recent study of coyote foraging in the Yukon, where voles were the most common alternative prey in the diet (O'Donoghue 1997), carrion was the most commonly-used alternative prey in our study area. This was surprising, considering voles were the most abundant food source by the end of the hare decline and carrion represented a negligible component of available prey biomass. Occurrence of voles in scats doubled as hares declined and was likely influenced by hare abundance, but voles ranked only fourth in dietary importance when hares were scarce. Coyote selection for voles did not increase in response to the hare decline or the vole irruption, contrary to the predicted response of a prey-switching generalist. A coyote would have to catch approximately 53 voles to equal the biomass of one snowshoe hare, and since voles occur primarily in meadows and snowshoe hares prefer dense brush, coyotes cannot search efficiently for hares and voles at the same time. Thus, the high total biomass of voles in the study area did not appear to raise their net profitability above that of less abundant prey types.

The strong selection for carrion during all years, on the other hand, suggests that carrion had high intrinsic and net profitability. Carrion does not need to be pursued and hunted down, so the handling costs of this prey item are low. After a carcass was discovered, coyotes returned to it repeatedly (unpubl. tracking data), so it was a reliable food source that required little search

time. However, use of carrion increased as hare abundance declined, suggesting that use of carrion had some costs, relative to use of hares. Wolves and humans (providers of the carrion) are known to kill coyotes (Polis et al. 1982, Paquet 1992, Switalski 2003, Wilmers et al. 2003), whereas the risks associated with hunting hares are minimal. Furthermore, carrion may be nutritionally inferior to live prey because wolves typically leave little meat: in my study area, scavengers were often left with little more than the hide, stomach contents, and bones.

Unlike carrion, Dall sheep and ground squirrels were minor components of the coyote diet in all years, and consumption of sheep was not related to hare or sheep abundance. Thus, variation in per-capita coyote predation on Dall sheep may be affected more by weather or sheep condition (Windberg and Mitchell 1990, Delgiudice 1998, Patterson and Messier 2000) than by prey abundance. Most coyote predation on Dall sheep occurred during the spring lambing season (Arthur 2003), when young lambs were most vulnerable and coyotes were rearing pups in high-elevation dens. Although coyotes did kill some lambs during winter, they appeared to require particular snow conditions (deep drifts) in order to effectively hunt sheep. Dall sheep may therefore be effectively unavailable to coyotes during most of the year, as are ground squirrels (which hibernate from September–April; Forsyth 1999). The ephemeral nature of these resources may partially explain why coyote selection for Dall sheep and ground squirrels did not increase when hares declined.

When hares were at peak abundance, coyote consumption of porcupine was rare. This finding was expected, given the scarcity of porcupine sign in the area and the danger associated with hunting porcupines: two radiocollared coyotes in this study area evidently died as a result of ingesting porcupine quills (ADF&G, unpubl.). Despite these considerations, coyote utilization of porcupines increased 25-fold in response to the hare decline. Similarly, Thurber et al. (1992) found that porcupines were the most common alternative prey for coyotes during a cyclic low in snowshoe hare numbers on the Kenai Peninsula in Alaska. I cannot rule out the possibility that coyotes increased consumption of porcupines due to an irruption in porcupine numbers, because I did not assess porcupine populations. This seems unlikely, however, because sightings of porcupines and porcupine tracks were infrequent and did not increase during the study. In addition, porcupines only have one young per year (Woods 1973), which limits their capacity for rapid population growth. Adult porcupines weigh approximately 7.5 kg (Zimmerling 2001), which is approximately equivalent to six snowshoe hares or 342 voles. Porcupines may therefore be a profitable meal in terms of biomass, but the mortality risk associated with hunting porcupine may outweigh the

potential reward unless the coyote is facing starvation. Avoidance of porcupine during years with abundant hares may represent risk-sensitive foraging by coyotes (Caraco et al. 1989, Brown 1999, Bateson 2002), and in this case the risk comes from the prey itself rather than another predator.

Community stability

Coyote predation on alternative prey species was not density dependent and should therefore be destabilizing. For example, the lack of feedback between coyote and Dall sheep population dynamics could allow coyotes to drive sheep populations extinct. Because coyotes rely primarily on hares but are major predators of lambs (Scotton 1998, Arthur 2003), they could drive sheep populations to low levels without suffering adverse consequences. Porcupines experienced a 25-fold increase in predation pressure during the hare decline, and coyote predation may therefore have caused porcupine populations to decline. Such a case was reported in the Great Basin Desert, when cougars switched from mule deer to porcupines and caused their near-extinction (Sweitzer et al. 1997).

The cyclic dynamics of snowshoe hares may prevent coyotes from driving alternative prey extinct in northern areas, however, because heavy predation pressure should be periodic rather than sustained. Instead, coyote predation may trigger cycles in alternative prey populations. Such secondary predator-driven population cycles have been reported for several species in northern ecosystems, such as greater snow geese (Bêty et al. 2002), ptarmigan, and ground squirrels (Boutin et al. 1995).

Assuming that the net profitability of available prey determines predator diet choice, I hypothesize that predation will increase the stability of a prey community only if net profitability is determined primarily by prey abundance. Positive frequency-dependent predation (i.e. selectively preying upon the most abundant prey), which is the mechanism by which generalist keystone predators stabilize prey populations, should only occur in situations where the most profitable prey is the most abundant prey. In order for abundance to be the main factor determining net profitability, the intrinsic profitabilities of available prey items must be similar. Measuring intrinsic profitability is extremely difficult in most natural situations, but prey size is a major component of profitability (Werner and Hall 1974, Sutherland 1982, Sinclair et al. 2003) and may help to predict the impact of predators on community dynamics. For example, coyotes that exhibited frequency-dependent predation in Texas were choosing from several similarly-sized rodents (Henke and Bryant 1999), whereas the sizes of

coyote prey in my study area varied by several orders of magnitude.

The specialist–generalist dichotomy

Although coyotes are classified as generalist predators, their foraging behavior and population dynamics in northern areas are driven primarily by snowshoe hare abundance, and in this sense they may function as specialists on snowshoe hares. The distinction between specialist and generalist predators may be somewhat artificial for several reasons. Predators may change from foraging as specialists to foraging as generalists as conditions change, both within and between communities (Krivan 1996), and individual predators within populations may vary in their degree of diet specialization (Bolnick et al. 2003). In addition, these terms are not well defined: specialist predators rely primarily on one prey type but often consume alternative prey (e.g. *Lynx canadensis*, O'Donoghue et al. 1998a), so it is unclear how wide a predator's diet niche must be in order to be categorized as a generalist (Roper 1994). In terms of predicting the effect of predators on community dynamics, the dichotomy may illuminate some broad-scale patterns (Murdoch et al. 2002) but may not be as useful when examining communities in detail. My study suggests that further examination of the behavior of predators in relation to characteristics of their prey could lead to new insights relevant to community ecology.

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