

Dietary breadth and overlap among five sympatric prairie carnivores

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Abstract

Ecological communities are shaped, in part, by the manner in which similar species consume and partition food resources. To better understand the structure of a mammalian carnivore community from a prairie habitat in central North America, we determined the dietary breadth and overlap of sympatric American badgers *Taxidea taxus*, coyotes *Canis latrans*, red foxes *Vulpes vulpes*, raccoons *Procyon lotor* and striped skunks *Mephitis mephitis*, via stomach content analysis of 411 carcasses salvaged as part of a predator control program in southern Saskatchewan, Canada (2000–2001). Carnivores consumed a total of 25 separate food items; for all species except raccoons, the majority of stomachs contained mammals, whereas other foods such as amphibians, bird remains and insects were also recovered. Raccoon stomachs tended to contain wheat seed, eggshells and birds. Dietary breadth varied among the five carnivore species, being narrowest for raccoons and widest for skunks. Overall, dietary overlap tended to be highest for species pairings associated with the highest level of presumed niche similarity, which included raccoon–skunk and coyote–fox dyads. Yet, levels of dietary overlap exhibited notable interannual variability for most species pairings. The assessment of a larger assemblage of carnivores within a North American prairie community shows that marked interspecific and temporal variation in dietary breadth and overlap may characterize a guild of sympatric species occupying similar habitat.

Introduction

One of the basic tenets of community ecology is that sympatric species occupying a common trophic level tend to exhibit niche differentiation and resource partitioning (Pianka, 1969; Schoener, 1974, 1986). Among the most important modes of resource partitioning in ecological communities is the differentiation of food resources, such that cases of extensive dietary overlap between similar species are limited. Questions concerning dietary breadth and overlap among carnivore guilds may be especially problematic, however, given the inconsistency in the distribution and abundance associated with many of their prey species, temporal or demographic variability in prey vulnerability to predation, the influence of intra- as well as interspecific competition on carnivore food habits and even the potentially strong individual-based variability in carnivore food preference (Maddock & Perrin, 1993; Wu, 1999). Accordingly, patterns of resource partitioning characterizing resident carnivore populations within particular ecological communities may be complex and dynamic.

For North American carnivores, the literature is replete with analyses of dietary breadth and overlap between species pairs or triads (e.g. Witmer & DeCalesta, 1986; Major & Sherburne, 1987; Litvaitis & Harrison, 1989; White, Ralls & Vanderbilt White, 1995; Kitchen, Gese & Schauster, 1999; Neale & Sacks, 2001a). Many of these studies have explained dietary differences within the context of alternative feeding strategies (i.e. generalist vs. specialist foraging) or intrinsic niche differentiation (i.e. disparity in habitat requirements or body size) (Rosenzweig, 1966; Schoener, 1974; Brown, 1975; Tokeshi, 1999). However, not all species fall into such discrete categories (Fox & Morrow, 1981). Indeed, within a given community, the relative breadth of a particular carnivore's diet (and by extension levels of interspecific dietary overlap) is arguably best defined in relation to the feeding habits manifested by its trophic counterparts. Thus, insofar as many previous analyses have likely painted an incomplete picture of dietary relationships among carnivores, future studies should seek to monitor more complete assemblages of these species in order to better understand patterns of community structure and function.

The prairies of North America are characterized by a diverse array of resident mammalian carnivore species. Among these, badgers *Taxidea taxus*, coyotes *Canis latrans*, red foxes *Vulpes vulpes*, striped skunks *Mephitis mephitis* and raccoons *Procyon lotor* are known to coexist along the prairie–agricultural interface, where they can occur at relatively high densities (Sargeant & Arnold, 1984; Messick, 1987; Rosatte, 1987; Sanderson, 1987; Voigt, 1987; Voigt & Berg, 1987). Most prairie carnivores have conventionally been considered to be opportunistic or generalist feeders (Bekoff, 1977; Wade-Smith & Verts, 1982; Larivière & Pasitschniak-Arts, 1996; Sovada, Roaldson & Sargeant, 1999; Chamberlain, Conner & Leopold, 2002). However, the five aforementioned predators are known to (1) exhibit disparate prey choice patterns (e.g. Dion, Hobson & Larivière, 1999; Greenwood *et al.*, 1999) and (2) rely upon a prey base that is both diverse and spatio-temporally variable. Thus, differences in their specific feeding patterns, and in particular interspecific variability with respect to dietary breadth and niche overlap, are likely to exist.

We studied the dietary breadth and overlap among the above five species of carnivores as part of a larger effort to determine the role of carnivores on nesting success of prairie waterfowl. Specifically, we used stomach content analysis to determine diet composition and evaluate whether prairie carnivore species: (1) differed in their dietary breadth, and (2) showed greater dietary overlap among pairs of species occupying presumably similar ecological niches (e.g. coyote–fox, skunk–raccoon). From a community perspective, we also predicted that any temporal changes in dietary breadth of carnivores would be associated with corresponding changes in dietary overlap between pairs of species.

Methods

Study area

The study was conducted *c.* 75 km south-west of Weyburn, SK, Canada (49°24'N, 104°39'). This area is in the Canadian Prairie Pothole Region, which includes about 480 km² of combined parklands, grasslands and wetlands (Johnson, Sargeant & Greenwood, 1989). Primary land use in the study area includes cultivation of cereal and oil seed crops, and livestock production. Most of the area is cultivated, although small parcels of native grassland pasture and hay production are present (<20% of entire area). The area is typified by rolling hills with a high density of semi-permanent, seasonal and ephemeral wetlands. Common native grassland plant species in the area include several grasses (*Agropyron* sp., *Bouteloua* sp., *Festuca* sp., *Hordeum* sp., *Koeleria* sp., *Poa* sp., *Stipa* sp.) and shrubs (*Symphoricarpos occidentalis*, *Rosa* sp., *Elaeagnus communitata*). During each year of study (2000 and 2001), predators were harvested in two randomly selected 41 km² sampling zones, spaced roughly 10 km apart. New sampling zones were chosen in 2001 that were >6 km from those used during the previous year. Importantly, we sought to ensure that the general hab-

itat characteristics remained consistent across the sampling zones for both years of the investigation.

Collection of specimens

During April–June 2000 and 2001, carnivores in the study area were collected as part of a predator control effort initiated by the Delta Waterfowl Foundation. On each sampling zone, badgers, coyotes, raccoons, red foxes and skunks were harvested by professional trappers using a combination of snares (primarily), foothold traps, cage-type live traps and opportunistic shooting. Upon capture, carnivore species, capture date and animal sex were recorded. The stomachs and intestinal tracts of all harvested animals were extracted and frozen before laboratory analysis. All predator removal procedures conformed to standard protocols and were approved by the University of Saskatchewan Animal Care Committee (UCACS protocol #20010055). Note that carcasses used in the present analysis were salvaged following the predator control program, and thus no animals were killed specifically for the purpose of this research.

Laboratory analysis of food habits

Samples were thawed, and intestinal tracts were sectioned (duodenum, ileum, jejunum) and opened longitudinally. Stomachs and intestinal walls were rinsed under running water whereas food contents were collected in a 600 µm sieve and placed in petri dishes to be air-dried. Examination of the contents of dried food items was performed using dissecting and compound scopes. Food contents were separated and identified to genus and species using general morphologic features of hair (for mammals, see Adorjan & Kolenosky, 1969), as well as via comparison with reference material (for seeds, invertebrates and amphibians, see Martin & Barkley, 1961; Fromm, 1982; Arnett, 1993; Conant & Collins, 1998; Acorn, 2000).

Traps used to capture raccoons and skunks were sometimes baited with fish or infertile chicken eggs. Clearly, the consumption of such bait by carnivores captured in live traps (i.e. about 50% of raccoons and skunks) could have biased our diet composition results. However, because fish were absent from the study area (V. Lester, pers. obs.), the modest occurrence of this food item in raccoon and skunk stomachs was interpreted as bait consumption and therefore not included in our analyses. For eggshells, we did not differentiate between those from chicken versus native birds, but because <5% of all traps were baited with chicken eggs in either year of study (S. Larivière, pers. obs.), we retained eggs as a food item in analyses. Yet, it is important to note that because our analysis was restricted to determining the presence/absence of food items in carnivore stomachs (see below), it is unlikely that bait consumption would have substantially affected our estimation of the relative importance of the remaining food types in carnivores.

Data analysis

To compare the relative consumption of prey among species and between years, we determined the frequency of occurrence of food items in stomachs (Kitchen *et al.*, 1999; Sovada, Roy & Telesco, 2001). To account for instances where multiple items were recovered from a single stomach, we calculated the relative frequency of occurrence of each food item (i.e. Hidalgo-Mihart *et al.*, 2001; Neale & Sacks, 2001a). Initially, we classified food items into 10 major categories: mammals, birds, amphibians, insects, wheat, eggshells, fish, leaves/fiber, grass and other (bones, sand, wood material, non-insect invertebrates, plastic and seeds/crops other than wheat). Ultimately, we limited our statistical analysis to prey items that occurred in $\geq 2\%$ of samples for each species in both years combined, which comprised six major categories (mammals, birds, amphibians, insects, wheat and eggshells). From these categories, we selected 25 food items to analyze dietary breadth and overlap. We used χ^2 analyses to compare the frequency of occurrence of food items between years and among species, and Fisher's exact tests when expected values were < 5 . Note that sample sizes were low for some species/year combinations, and thus statistical power is reported for analyses of interannual variability in diet. When performing multiple comparisons of food consumption among mammals, we used Bonferroni's correction to minimize the likelihood of Type I statistical error (Oehlert, 2000). All tests were performed using Systat software (Systat, 2000).

We calculated measures of niche breadth (Smith, 1982) using the relative frequency of occurrence of food items [where $FT = \sum (\sqrt{p_j a_j})$, where FT is Smith's measure of niche breadth, p_j the fraction of items in the diet that are of food category j and a_j the proportion of total resources comprised by resource j]. Smith's measure of niche breadth is a standardized measure varying from 0 (minimal) to 1.0 (maximal) that is relatively insensitive to selectivity for rare resources (Franzreb, 1984; Krebs, 1999; Hofer, Baur & Bersier, 2003). Use of this index enabled us to (1) quantify the extent to which carnivore-specific food-selection patterns focused on particular food categories, (2) assess the consistency of these food-selection patterns between the 2 years of study and (3) evaluate the uncertainty of our es-

timates using 95% confidence intervals. Importantly, we obtained results qualitatively similar to those presented herein when using Levins' index (Levins, 1968). To analyze the overlap in food use among the five species and between years, we used the Renkonnen index [$P = \sum \text{minimum}(p1_i, p2_i)$], where P is the percentage similarity between samples 1 and 2, $p1_i$ the percentage of species i in community sample 1 and $p2_i$ the percentage of species i in community sample 2] of percentage overlap (see Krebs, 1999), using the relative frequency of occurrence of food items in our samples. To further investigate the similarity between carnivore species and evaluate diet overlap in the context of the relative abundance of the six major food groups, we correlated the overall frequency of occurrence of food categories between species pairs (see Neale & Sacks, 2001a). The correlation coefficient (r) was considered an index of overall dietary similarity.

Results

We analyzed 411 intestinal tracts during the course of the study, with 186 animals being taken in 2000 and 228 in 2001. Among the carcasses examined, 42.8% were striped skunks ($n = 176$), 27.7% were raccoons ($n = 114$), 12.4% were badgers ($n = 51$), 9.7% were foxes ($n = 40$) and 7.3% were coyotes ($n = 30$).

Occurrence and abundance of food items

The five carnivore species consumed a total of 25 separate food items, constituting the six major food categories (mammals, insects, eggshells, birds, wheat and amphibians) that were used in subsequent analyses. The overall mean per cent frequency of occurrence for the five most common carnivore food categories (carnivore species and years combined) was $54.7 \pm 18.6\%$ (\pm se) for mammals, $34.0 \pm 29.7\%$ for insects, $30.5 \pm 13.0\%$ for eggshells, $29.2 \pm 14.1\%$ for birds and $12.2 \pm 18.2\%$ for wheat (Table 1). Combined, eggshells and birds were recovered from $59.8 \pm 13.9\%$ of stomachs, and across predator species this percentage ranged from 43.1% for badgers to 78.9% for raccoons.

A total of 13 mammal species was recovered from carnivore stomachs. In general, consumption of mammals was different among the five carnivore species ($\chi^2 = 53.2$,

Table 1 Frequency of occurrence of major food types (six) in stomachs of badgers (B), coyotes (C), foxes (F), raccoons (R) and skunks (S)

Food items	2000					2001					Overall 2000/2001				
	B (18)	C (9)	F (13)	R (47)	S (97)	B (33)	C (21)	F (27)	R (67)	S (79)	B (51)	C (30)	F (40)	R (114)	S (176)
Mammals	44.4	33.3	46.1	27.7	58.7	81.8	76.2	66.7	17.9	60.8	68.6	63.3	60.0	22.0	59.6
Amphibians	11.1	0	0	10.6	40.2	3.0	0	0	2.9	7.6	5.9	0	0	6.1	25.5
Insects	5.5	11.1	15.4	36.2	78.3	12.1	23.8	7.4	44.8	88.6	16.1	20.0	10.0	41.2	82.9
Wheat seeds (<i>Triticum</i> spp.)	11.1	11.1	7.7	55.3	3.1	0	4.8	0	37.3	3.8	3.9	6.7	2.5	44.7	3.4
Eggshells	27.7	11.1	15.4	38.3	20.6	39.4	23.8	14.8	53.7	51.9	35.3	20.0	15.0	47.4	34.9
Birds	11.1	33.3	53.9	21.3	22.7	6.1	28.6	44.4	38.8	36.7	7.8	30.0	47.5	31.6	29.0
Birds and eggshells combined	38.3	44.4	69.2	59.6	43.4	45.4	52.4	59.3	92.5	88.6	43.1	50.0	62.5	78.9	64.7

Number of stomachs analyzed is in parentheses.

Table 2 Relative frequency of occurrence of all food types in stomachs of badgers (B), coyotes (C), foxes (F), raccoons (R) and skunks (S)

Food items	2000					2001				
	B (18)	C (9)	F (13)	R (47)	S (97)	B (33)	C (21)	F (27)	R (67)	S (79)
<i>Mammals</i>	51.8	27.3	42.8	15.7	22.6	55.5	51.4	52.6	7.0	23.8
Meadow vole <i>Microtus pennsylvanicus</i>	11.1	0	14.3	5.6	3.8	15.5	20.0	26.3	2.8	5.7
Deer mouse <i>Peromyscus maniculatus</i>	3.7	0	4.7	2.2	2.9	8.9	2.8	2.6	0	3.6
Red-backed vole <i>Clethrionomys gapperi</i>	7.4	0	4.7	4.5	4.2	11.1	2.8	2.6	1.4	9.3
Meadow jumping mouse <i>Zapus hudsonius</i>	7.4	0	4.7	1.1	10.0	2.2	0	0	0	0.5
Lemming (<i>Synaptomys</i> spp.)	7.4	0	0	0	0	2.2	0	0	0	1.5
Red squirrel <i>Tamiasciurus hudsonicus</i>	7.4	0	4.7	2.2	0.4	6.7	0	2.6	0.7	0.5
Eastern chipmunk <i>Tamias striatus</i>	3.7	0	4.7	0	0.4	6.7	0	0	0	0
Ground squirrel (<i>Spermophilus</i> spp.)	0	0	0	0	0	0	5.7	0	0	0.5
Fox squirrel (<i>Sciurus</i> spp.)	0	0	0	0	0	2.2	8.6	10.5	0.7	0
Snowshoe hare <i>Lepus americanus</i>	3.7	9.1	0	0	0	0	0	0	0	0
Deer (<i>Odocoileus</i> spp.)	0	18.2	0	0	0	0	5.7	0	0	0
Porcupine <i>Erethizon dorsatum</i>	0	0	4.7	0	0.4	0	2.8	0	0	0
Shrew (<i>Sorex</i> spp.)	0	0	0	0	0.4	0	0	0	0.7	2.1
Muskrat <i>Ondatra zibethicus</i>	0	0	0	0	0	0	2.8	5.2	0	0
<i>Amphibians</i>	7.4	0	0	4.5	13.0	2.2	0	0	0.7	2.1
Tiger salamander <i>Ambystoma tigrinum</i>	7.4	0	0	1.1	1.7	2.2	0	0	0	0
Unknown salamander	0	0	0	0	2.9	0	0	0	0	0
Chorus frog <i>Pseudacris triseriata</i>	0	0	0	0	4.2	0	0	0	0.7	2.1
Tree frog (<i>Hyla</i> spp.)	0	0	0	1.1	0.4	0	0	0	0	0
Wood frog <i>Rana sylvatica</i>	0	0	0	2.2	3.8	0	0	0	0	0
<i>Insects</i>	7.4	9.1	9.5	19.1	45.6	8.9	14.3	10.5	21.1	36.3
Coleoptera	3.7	0	0	14.6	19.2	4.4	11.4	5.2	16.2	19.7
Orthoptera	3.7	0	9.5	3.4	25.5	4.4	0	0	4.2	16.1
Other insects (Lepidoptera, Hymenoptera)	0	9.1	0	1.1	0.8	0	2.8	0	0.7	0.5
Wheat seeds	7.4	9.1	4.7	29.2	1.2	0	2.8	0	17.6	1.5
Eggshells	18.5	9.1	9.5	20.2	8.4	28.9	14.3	10.5	25.3	21.2
Birds	7.4	27.3	33.3	11.2	9.2	4.4	17.1	31.6	18.3	15.0

Number of gastrointestinal tracts examined is in parentheses.

d.f. = 4, $P < 0.001$), mostly due to the low use of this food item by raccoon (Table 1). Badgers relied most heavily on mammalian prey, followed by coyote, fox, skunk and raccoon (overall 2-year consumption = 68.6% of all stomachs contained in mammals; Table 1). For badger, fox and raccoon, meadow voles *Microtus pennsylvanicus* were the most commonly recovered species in 2000 and 2001; coyotes consumed deer most frequently in 2000 and meadow voles most often in 2001, whereas skunks consumed meadow jumping mouse *Zapus hudsonius* most frequently in 2000 and red-backed voles *Clethrionomys gapperi* most often during 2001 (Table 2). Although all carnivores consumed a number of small mammals other than voles, skunks and foxes appeared to have the greatest diversity of rodent species in their diet (Table 2). The frequency of mammal occurrence increased between years only for badgers ($\chi^2 = 7.56$, $P = 0.006$, power = 0.51). When carnivore species were compared collectively, interannual variability in the consumption of mammals existed only for badgers.

Consumption of insects was different among carnivores ($\chi^2 = 149.3$, d.f. = 4.0, $P < 0.001$), with skunks consuming insects with greater frequency than the remaining carnivores (overall 2-year consumption = 82.9%; Table 1). Insects

belonging to the taxonomic families Orthoptera and Coleoptera were most commonly encountered, especially among skunk and raccoon (Table 2). Although insects occurred more frequently during 2001 for four of the five predator species (Table 1), no interannual differences in the consumption of insects were observed (all $P > 0.58$).

Consumption of birds differed among carnivores ($\chi^2 = 18.1$, d.f. = 4.0, $P = 0.001$). Bird remains were more common in foxes than for the remaining carnivore species (overall 2-year consumption = 47.5%; Table 1). Although raccoons and skunks had a higher frequency of bird feathers in the second year ($P < 0.05$), the power of the tests was low (power < 0.20). For the remaining three species, there was no interannual variability in the occurrence of bird feathers (all $P > 0.61$; Tables 1 and 2).

Carnivore species also differed in their consumption of eggs ($\chi^2 = 17.6$, d.f. = 4.0, $P = 0.001$). Eggshell fragments were most commonly found in raccoon stomachs (overall 2-year consumption = 47.4%; Table 1). In contrast, such fragments were rarely recovered from fox and coyote stomachs (Table 1), and interannual variability in the occurrence of eggshells was observed only for skunks ($\chi^2 = 18.81$, $P < 0.001$, power = 0.69).

Wheat seeds were clearly most prevalent in raccoon stomachs (overall 2-year consumption = 44.7%; Table 1) compared with other carnivores ($\chi^2 = 108.5$, d.f. = 4.0, $P < 0.001$). Raccoons exhibited substantive variation in wheat consumption between years (Tables 1 and 2; $\chi^2 = 3.62$, $P < 0.057$, all other $P > 0.12$); however, the power of the test was low (power = 0.25).

Amphibians were present in the diets of badgers, raccoons and skunks during both years, with skunks apparently consuming amphibians to the greatest extent and coyotes and foxes not consuming them at all (Table 1). The absence of amphibians from coyote and fox diets contributed to the observed difference in this food between carnivores ($\chi^2 = 40.95$, d.f. = 4.0, $P < 0.001$). Chorus frog *Pseudacris triseriata* was the most commonly encountered amphibian in skunk stomachs, whereas badgers consumed tiger salamanders *Ambystoma tigrinum* and raccoons ate a greater diversity of amphibian species including treefrogs (*Hyla* spp.) and wood frogs *Rana sylvatica* (Table 2). Interannual differences in amphibian consumption were detected only for skunks ($\chi^2 = 22.92$, $P < 0.001$, power = 0.40; Table 2).

Dietary breadth and overlap

Smith's (1982) niche breadth index, using the suite of 25 separate food items, indicated that dietary breadth was narrower for coyotes, foxes and raccoons than for the remaining two carnivore species in 2000 (Table 3). This pattern was not repeated in 2001, when only foxes and raccoons manifested restricted dietary patterns (Table 3). In 2000, badgers and then skunks were characterized by the broadest diet, whereas in 2001, coyotes, badgers and skunks showed the most generalized diet (Table 3). When the 2 years of the study were combined, skunks and then badgers were characterized by the greatest dietary breadth (Table 3). Coyotes were the only species to manifest a temporal shift in dietary breadth, primarily because of increased consumption of mammals during the spring of 2001 (Tables 2 and 3). Notably, our sample for coyotes was small during spring 2000, which might have influenced our observation of greater dietary breadth for this carnivore species for spring 2001.

With both years of the study pooled, the extent of dietary overlap (measured using the Renkonnen index) characterizing all possible carnivore pairings ranged from 44.7% for the fox–skunk pairing to 66.9% for the coyote–fox pairing

(Table 3). The highest levels of dietary overlap were recorded for coyote–fox, raccoon–skunk and badger–fox pairings; the lowest values were associated with the fox–skunk, fox–raccoon and coyote–skunk pairings (Table 3). Per cent dietary overlap was lower among most carnivore pairings in 2000 (seven pairs) than in 2001; however, levels of overlap characterizing the badger–fox, badger–raccoon and fox–raccoon pairings were higher in the study's first year. Pairings featuring the highest levels of per cent overlap also varied temporally: in spring 2000, per cent overlap values were highest for badger–fox, badger–raccoon and raccoon–skunk pairings; the following year, per cent overlap values were highest for the coyote–fox, raccoon–skunk and badger–skunk pairings (Table 3).

Our index of overall dietary similarity with respect to use of the six designated food categories [expressed using a correlation coefficient (r)] indicated slightly different trends in carnivore dietary overlap. Specifically, this index revealed a close dietary correlation for only coyote–fox (both years), badger–coyote and badger–fox (spring 2001) pairings (all $P < 0.1$; Table 4).

Discussion

The results of this analysis generally support the contention that assemblages of sympatric carnivore species should exhibit variability in dietary breadth and overlap that is consistent with general principles of resource partitioning and niche delineation within ecological communities. Among the five carnivores studied, interspecific differences were observed; specifically, overall dietary breadth values were relatively high for skunks and badgers, intermediate for coyote and fox, and low for raccoons (Table 3). Moreover, as predicted, two of the three species pairs presumably sharing ecological niches (coyote–fox, skunk–raccoon) manifested the highest recorded degree of dietary overlap as measured using the Renkonnen index; similarly, two of the three pairs ostensibly characterized by high niche overlap (badger–coyote, coyote–fox) were the only pairs to show significant overlap when analyzed using the correlative index.

Occurrence and abundance of food items

Among the carnivores assessed, four species (badgers, coyotes, foxes and skunks) preyed heavily on a wide variety of

Table 3 Niche breadth [possible range 0–1, calculated using Smith's (1982) index] and percentage of dietary overlap (calculated using Renkonnen index; Krebs, 1999) among badgers (B), coyotes (C), foxes (F), skunks (S) and raccoons (R) in southern Saskatchewan

	Dietary breadth					Percentage of overlap									
	Badger	Coyote	Fox	Raccoon	Skunk	B–C	B–F	B–R	B–S	C–F	C–R	C–S	F–R	F–S	R–S
2000	0.75	0.51	0.65	0.66	0.72	29.6	58.2	57.3	45.2	47.6	34.6	19.7	45.3	40.9	53.2
95% CI	0.57–0.88	0.21–0.76	0.42–0.83	0.55–0.76	0.67–0.80										
2001	0.68	0.69	0.59	0.59	0.67	46.7	47.3	47.9	55.8	69.2	52.0	54.7	42.6	43.8	67.9
95% CI	0.55–0.80	0.53–0.83	0.43–0.73	0.49–0.68	0.58–0.75										
Combined	0.74	0.72	0.69	0.65	0.75	47.3	54.7	52.4	50.2	66.9	52.8	46.2	45.6	44.7	59.9
95% CI	0.64–0.83	0.58–0.83	0.57–0.80	0.58–0.72	0.69–0.80										

Confidence intervals (95%) were calculated according to Smith (1982).

Table 4 Linear regression of the relative importance of frequency of occurrence of the six major food items among badgers, coyotes, foxes, skunks and raccoons in southern Saskatchewan

Interaction	2000			2001		
	<i>r</i>	RMSE	<i>P</i>	<i>r</i>	RMSE	<i>P</i>
Badger–coyote	0.49	14.36	0.32	0.91	14.98	0.01
Badger–fox	0.42	14.93	0.40	0.74	23.72	0.09
Badger–raccoon	0.04	16.48	0.94	0.09	35.41	0.86
Badger–skunk	0.10	16.41	0.84	0.47	31.43	0.35
Coyote–fox	0.98	2.92	0.00	0.92	12.10	0.01
Coyote–raccoon	0.07	15.15	0.88	0.05	30.22	0.93
Coyote–skunk	0.06	15.16	0.90	0.57	24.85	0.24
Fox–raccoon	0.22	23.71	0.67	0.12	30.34	0.83
Fox–skunk	0.11	24.19	0.84	0.35	28.58	0.49
Raccoon–skunk	0.34	16.21	0.51	0.43	18.90	0.39

The pairwise coefficient of correlation is represented by *r*; RMSE is the root mean square error.

mammals. By contrast, raccoon stomachs contained mammal remains infrequently, and instead this carnivore appeared to commonly ingest birds, eggs (presumably as a result of nest predation) and plant material (in particular, wheat seeds). Skunks, and to a lesser extent badgers and foxes, often included insects in their diet, whereas skunks also appeared to prey heavily on amphibians. These findings are generally consistent with previous reports concerning dietary composition of the five study species in central North America (e.g. Sargeant & Arnold, 1984; Messick, 1987; Rosatte, 1987; Sanderson, 1987; Voigt, 1987; Voigt & Berg, 1987). Interestingly, we rarely documented interannual fluctuation in the use of particular food categories, suggesting that patterns of prey availability for the carnivores assessed may have been relatively stationary over the 2 years of the investigation. For example, a closer look at the interannual variation in use of mammals by the four carnivore species other than coyotes (Table 2) fails to reveal evidence for substantive temporal changes in small mammal occurrence. In particular, consumption of voles, a small mammal species for which dramatic numerical fluctuations across much of North America have been documented (Johnson & Johnson, 1982), was remarkably consistent during the study.

Dietary breadth and overlap

Feeding specialization has been described as 'use of a relatively narrow portion of the resource spectrum' (Cody, 1974) or 'the stable use of a particular food type irrespective of fluctuations in the availability of that food type' (Kruuk & Parish, 1981). With these traditional definitions providing a conceptual framework, several carnivore species have been shown to exhibit rather pronounced feeding specialization (e.g. Martín, Rodríguez & Delibes, 1995; Fedriani, Ferras & Delibes, 1998). However, when prey abundance fluctuates dramatically over a period of time, even alleged specialist species may exhibit more generalist feeding patterns (e.g. O'Donoghue *et al.*, 1998). Moreover, a review of dietary

breadth among herbivorous insects revealed that while generalization characterized the diet of many insect species, the dietary choices of individuals within particular populations were often specialized (according to the traditional framework described above), suggesting that in many cases dietary breadth may be a local (i.e. system-specific) phenomenon rather than an immutable species characteristic (see Fox & Morrow, 1981).

Although spatio-temporal patterns of prey availability were not assessed, our results show that analyses involving multiple sympatric carnivore species (occupying a similar trophic level within an ecological community) can provide insights that would be missed by simpler dietary investigations focusing on species pairs or triads. The five carnivores studied are believed to be generalists (according to the traditional framework), and accordingly each manifested intermediate levels of dietary breadth. Thus, studies of these carnivores in isolation or as pairs would be likely to underestimate actual levels of variability characterizing their dietary breadth. For example, when analyzed individually, the Eurasian badger *Meles meles* has been characterized extensively as an opportunistic feeder (Kruuk & de Kock, 1981; Martín *et al.*, 1995; Fedriani *et al.*, 1998) acting locally as a specialist based on the availability of prey resources, even though variations in temperature and food resources can force this carnivore to diversify its diet and therefore behave more as a generalist carnivore (Sidorovich *et al.*, 2000). Here, in evaluating them simultaneously, we show that a range in diet breadth does exist; namely, over the course of our investigation, skunks and badgers manifested similar generalized feeding patterns relative to other species in the community, whereas raccoons and foxes were characterized by the most specialized diet. Frequency estimates for occurrence of food in stomachs do not account for relative biomass, and we acknowledge that use of an index incorporating biomass information may have led the five carnivores under investigation to be rated differently in terms of niche breadth. Nevertheless, it is clear that the interpretation of diet breadth analyses can be subject to

influence from the feeding behavior of other species in the analysis, and thus should be considered as context specific.

In addition to notable diet breadth variability, we found large interspecific differences in dietary overlap that, in many cases, coincided with presumed levels of niche similarity. Based on a review of the literature (Scott-Brown, Herrero & Reynolds, 1987; Kitchen *et al.*, 1999; Neale & Sacks, 2001a), we predicted that coyotes would compete strongly with foxes and perhaps badgers for mammalian prey, and consequently that the coyote–fox and coyote–badger pairings would be characterized by high levels of dietary overlap. We predicted that high dietary overlap would characterize the raccoon–skunk pairing as well, given that these species have been shown in the past to rely on similar prey items (e.g. waterfowl nests; see Lokemoen *et al.*, 1982; Greenwood, 1986; LaGrange *et al.*, 1995). Accordingly, using two different indices, we found that the majority of pairings (four of five, years pooled) associated with significant dietary overlap were in fact those sharing similar niches. The considerable overlap characterizing the diets of coyotes and foxes, due primarily to heavy mutual reliance on small mammals, indicates that resource competition between these two species may be severe. However, coyotes relied more heavily on ungulates and lagomorphs, whereas foxes preyed more heavily on small rodents; these dietary specializations may have alleviated overall levels of competition between canid species. This pattern of exclusive use of particular prey items, despite overall dietary similarity, also characterizes the relationships between sympatric coyotes and gray foxes *Vulpes velox* (Kitchen *et al.*, 1999) or bobcats *Lynx rufus* (Neale & Sacks, 2001b). Interestingly, the raccoon–skunk pairing was found to have the second highest overlap using Renkonnen's index, but no overlap when using the correlative index of overall dietary similarity. A thorough examination of the diets of these two species over the course of this analysis (Table 2) shows apparently different patterns of prey selection: skunks used insects, amphibians and small mammals more extensively whereas raccoons were more reliant upon wheat seeds and eggs. Thus, our finding that these two carnivores manifested closely overlapping diets using Renkonnen's index may be suspect. More importantly, perhaps, this disparity underscores the variability that can typify different approaches to measuring dietary overlap, and suggests that future analyses of diet breadth should use multiple methods of measurement to reduce the likelihood of model-specific bias.

Measures of niche (i.e. diet) overlap should be used to determine, in a descriptive manner, the way an ecological community is organized (Abrams, 1980), and niche theory predicts that as species become more reliant on a limited number of food types (i.e. undergo a reduction in dietary breadth), their dietary overlap with other species in the community should decline (Tokeshi, 1999). Accordingly, we anticipated that dietary overlap between carnivores would be related to their dietary breadth during a given year. It is notable that, although badgers did not exhibit a significant temporal shift in diet breadth, a qualitative reduction in its usage of the food items analyzed in this study from 2000 to

2001 was associated with concomitant reductions in dietary overlap with two of its four counterparts.

A clear shortcoming of previous studies of diet breadth and overlap in carnivores is the lack of community-level analyses involving more than two or three species. This deficiency has led to a restricted view of the structure and function of ecological communities, and how these community attributes may be influenced by particular resource-use patterns. By virtue of our assessment of a larger assemblage of carnivores within a North American prairie community, we were able to show that notable interspecific and temporal variation in dietary breadth and overlap may characterize a group of sympatric species occupying similar habitats. Yet, our work also highlighted, by its absence, the need to monitor prey abundance concurrently with predator diet studies. Future work on this topic should be conducted extensively, in terms of both space and time, so that spatio-temporal changes in dietary habits can be assessed in the context of prey population change. Such multi-faceted research will further elucidate general patterns of resource partitioning and niche differentiation in ecological communities, and thus help improve our understanding of the mechanisms underlying species coexistence and community structure.

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