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PREY SWITCHING OF SYMPATRIC CANIDS IN RESPONSE TO VARIABLE PREY ABUNDANCE

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We investigated the effects of fluctuating prey numbers on the foraging strategies and potential mechanisms for coexistence of 2 sympatric predators, coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*), in a heterogeneous environment in northeastern Illinois. We quantified the availability of mammalian and avian prey across different habitats, analyzed scats collected along standardized routes for occurrence of prey items, and estimated the number and biomass of vertebrate prey consumed. Abundances of the most frequently consumed prey (voles, rabbits, and mice) differed significantly over time, especially in relation to an ice storm that occurred during the study. Coyotes and red foxes tended to select voles and rabbits in number, rabbits in biomass, and incorporated greater numbers and biomass of other prey such as deer, pheasants, and sciurids after the ice storm. Log-linear analyses indicated that both coyotes and red foxes exhibited switching behavior, with differential shifts among the number and biomass of alternative prey they consumed. Hence, foraging strategies of coyotes and red foxes appeared to be a combination of prey selectivity and switching behavior. Our study suggests that competition between coyotes and red foxes for similar primary prey species and limited environments to exploit at the urban–rural interface may contribute to displacement of red foxes by coyotes.

Key words: *Canis latrans*, competition avoidance, coyote, Illinois, log-linear analysis, prey selection, prey switching, red fox, *Vulpes vulpes*

Dietary resource partitioning is 1 strategy for coexistence between different carnivore species (Schoener 1974). For example, sympatric coyotes (*Canis latrans*) and swift foxes (*Vulpes velox*) have exhibited differences in diet based upon prey size selection and seasonal availability (Kitchen et al. 1999). Prey size preferences also have facilitated resource partitioning between sympatric coyotes and red foxes (*Vulpes vulpes*—Azvedo et al. 2006; Major and Sherburne 1987), coyotes and bobcats (*Lynx rufus*—Neale and Sacks 2001), gray wolves (*Canis lupus*) and coyotes (Arjo et al. 2002), and maned wolves (*Chrysocyon brachyurus*) and crab-eating foxes (*Cerdocyon thous*—Juarez and Marinho-Filho 2002). When prey are abundant, dietary differences among sympatric carnivores may be less apparent, with 2 or more predator species feeding upon the same prey (Gese et al. 1996b; Neale and Sacks 2001); a subsequent decrease in prey abundance would increase interspecific competition unless the predators choose different alternative prey.

Among vertebrate predators, fluctuations in prey abundance can induce functional responses or changes in the rate of prey consumption (Dale et al. 1994; Jaksic et al. 1992). This behavioral response can take the form of prey switching, a shift to consuming alternative food sources, especially when primary prey decline in abundance (Kjellander and Nordström 2003; Sundell et al. 2003), although this response may be influenced by prey preference (Murdoch 1969). Prey switching can affect reproductive success of predators (Kjellander and Nordström 2003; Rosenberg et al. 2003) and facilitate survivorship of their primary prey (Miller et al. 2006). In Scandanavia, switching by generalist predators between alternative small mammal prey helped to maintain stable predator populations and dampened fluctuations of the prey populations (Erlinge 1987; Erlinge et al. 1983). Korpimäki and Norrdahl (1991) showed that sympatric raptors fed mainly on 2 species of voles (*Microtus*) during high prey abundance but also consumed several other alternative prey. Thus, temporal fluctuations of prey populations cannot only evoke switching behavior, but may facilitate interspecific tolerance

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of sympatric predators. The ability to exploit alternative prey may be particularly important for carnivores in or near urban areas (Randa and Yunger 2006). This is because urban environments typically contain limited areas of open space suitable for wildlife, inducing overlap in resource use especially for large to medium-sized carnivores (Matthiae and Stearns 1981; Riley et al. 2003).

Coyotes and red foxes are canid predators that co-occur over much of their ranges in North America, including urban regions. Both predators have been considered dietary generalists with small mammals commonly comprising a major proportion of their food (Cypher 1993), creating the potential for dietary overlap. We investigated potential mechanisms of coexistence between coyotes and red foxes by examining their foraging behavior in relation to prey availability within a heterogeneous environment of an urban–rural interface, before and after a catastrophic ice storm. The heterogeneity of the study site supports a variety of potential prey whose densities fluctuate seasonally and noncyclically between years, including voles (*Microtus*—Getz et al. 1987; Meserve and Klatt 1985), mice (*Peromyscus*—Yunger 2002), and eastern cottontails (*Sylvilagus floridanus*—Mankin and Warner 1999). Seasonal variation in diet of coyotes (Andelt et al. 1987) and red foxes (Cook and Hamilton 1944) illustrates the potential of induced predator responses (i.e., switching behavior) to temporal variations in prey. Although switching behavior by predators has traditionally been described based on number of available prey, we compared diets of predators to both the number as well as the biomass of prey because biomass may better reflect caloric intake and importance of prey items in some predator diets (Cumberland et al. 2001).

We hypothesized that selection of primary prey species would differ between coyotes and red foxes when prey were relatively abundant; a significant decrease in availability of primary prey would lead coyotes and red foxes to switch predominantly to the most abundant prey; and upon switching, an overall difference in the diets of these sympatric predators would be maintained through the supplemental consumption of less-abundant alternative prey. The widespread occurrence of the ice storm dramatically reduced some of the potential prey species of these canids. We specifically predicted that diets of both predators would diversify after the ice storm and that shifts in the number and biomass consumed of various alternative prey would differ significantly between coyotes and red foxes.

Materials and Methods

Study site.—The study site was located at Fermi National Accelerator Laboratory (Fermilab) approximately 50 km due west from Chicago, Illinois (41°50′N, 88°15′W). Fermilab is near the urban–rural interface of the Chicago metropolitan area, encompasses approximately 2,800 ha, and is a heterogeneous area, marked by distinct habitat boundaries. The area surrounding Fermilab consisted of small open spaces of mainly agricultural land and woodland preserves interspersed with light industry and residential neighborhoods. We conducted our study at 7 different areas within Fermilab, representing 5 habitat types: a 14.1-ha old field, dominated by Queen Anne's lace (*Daucus carota*) and tall goldenrod (*Solidago altissima*); 2 tallgrass prairie sites (24.6 and 34.1 ha), dominated by big bluestem (*Andropogon gerardii*) and Indian grass (*Sorghastrum nutans*); a 24.8-ha bromegrass field, dominated by smooth brome (*Bromus inermis*); an 8.5-ha shrubby old field, dominated by gray dogwood (*Cornus racemosa*) and tall goldenrod with small stands of quaking aspen (*Populus tremuloides*); and 2 oak woodlands (8.6 and 31.4 ha), dominated by mature oaks (*Quercus* spp.). We chose these different habitats because they represented the heterogeneity of the study site and included all prey species potentially found in canid diets at Fermilab.

Prey availability.—We estimated small mammal species compositions and abundances by mark–recapture livetrapping from September 1993 through August 1995 along three 192-m transects placed within the core area in each sampling area. The transects were parallel and spaced 70–85 m apart to help maximize their independence in relation to small mammal movements, with at least 50 m between each transect and major changes in vegetation. Seventeen traps were placed at 12-m intervals along each transect, resulting in 51 traps per area. All study areas were trapped for 2 nights on a monthly basis using 23 × 9 × 7.5-cm Sherman live traps (H. B. Sherman Traps, Inc., Tallahassee, Florida) baited with peanut butter and rolled oats. We checked traps at dawn and about 1600 h and marked captured individuals with a uniquely numbered ear tag. All field procedures met the guidelines established by Northern Illinois University's Institutional Animal Care and Use Committee and guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

We used standardized, monthly diurnal visual counts to assess the abundance of ring-necked pheasants (*Phasianus colchicus*) and sciurids not captured in Sherman traps, as well as nocturnal spotlight counts for rabbits (eastern cottontails), in each of the 7 study areas. Trapping transects were extended to 250 m to account for the larger spatial movements of these animals. The counts were conducted immediately before and after each of the monthly small mammal trap sessions. We counted animals observed within 25 m while walking along the transect, taking care to avoid double-counting individuals potentially moving along or between transects. We obtained estimates of white-tailed deer (*Odocoileus virginianus*) abundance from winter helicopter surveys, which were sufficient for our prey availability comparisons because deer numbers do not fluctuate greatly within a 1-year period (Etter et al. 2002; Gladfelter 1984). The aerial counts were conducted during winter 1993–1994 at Fermilab and compared to deer abundances from surveys conducted in 1,330 ha of adjacent preserves, during the winters of 1993–1994 and 1994–1995. Deer were able to move among these preserves and Fermilab.

Predator diets.—Throughout the study site, we collected canid scats monthly along standardized routes (Krebs 2006;

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Pearson 1966) totaling 7.2 km. Based upon our previous observations of scat degradation from captive and wild canids, we discarded scats >1 month old at the beginning of the study. Scats were oven-dried to constant weight (approximately 24 h) and examined for bone and hair remains. We compared these remains to a reference collection and hair key (Moore et al. 1974), identifying mammalian prey to genus or species. We used the minimum count of diagnostic parts, primarily teeth, to ascertain the number of mammalian prey individuals per scat (Weaver and Hoffman 1979). We identified birds based upon feather and bone remains and used exoskeletons to identify arthropods. We distinguished coyote and red fox scats by size comparisons following Green and Flinders (1981) and Halfpenny (1986); mass of scat deposited in a single occurrence was a differentiating criterion in the event of size overlaps, which occurred in <5% of scats collected. Potential misidentification would reduce the likelihood of detecting significant dietary differences between canids.

We categorized vole skeletal remains in scat as juveniles and adults to determine age selection by coyotes. Patterns of tooth wear (Hinton 1926; Martin 1956) and cranial measurements have been used to age voles (Carleton 1985). We compared arvicoline prey remains to cranial reference material from individuals of known age. Differentiating criteria for conservative age estimates (juvenile versus adult) included size of molars, length of mandibular toothrow (which was shorter in very young individuals), degree of enamel and dentine degradation, and cranial measurements if available.

Data analysis.—Using Package CMR (Le Boulengé 1987), we calculated minimum number known alive (Krebs 1966) estimates of small mammal abundance across all 21 sampling transects for each month. We used the sum of individuals obtained from the visual count data across all transects for monthly abundances of each of the remaining prey. Deer abundances from the aerial surveys were adjusted for the area covered by all 21 sampling transects (250 × 50 m per visual count transect × 21 transects = 26.25 ha). We computed seasonal availability of each prey by summing monthly abundances across the following 3-month time blocks: winter (December–February), spring (March–May), summer (June–August), and fall (September–November). Summing prey abundance across all sampling transects for a given time period reflected the same scale at which predator scats were collected. Predator diets thus were compared to changes in prey availability across all sampling areas because coyotes and red foxes could move and forage throughout Fermilab.

We used SAS PROCEDURE GLM (SAS Institute Inc. 2007) to conduct analysis of covariance (ANCOVA) to test for differences in abundance among the prey; species served as the categorical predictor variable and time the covariate. An ice storm occurred in late January 1994, causing a sharp decrease in small mammal abundance and an extreme nonlinearity in the prey database. Hence, we used separate ANCOVAs for pre– (September 1993–January 1994) and post– (February 1994–August 1995) ice storm prey abundance. Statistical inferences were based on type III sum of squares (Littell et al. 1991).

We used log-linear analyses (SAS PROCEDURE CATMOD—SAS Institute Inc. 2007) to examine whether there was a significant difference between pre– and post–ice storm prey selection of coyotes and foxes, whether canids selected prey in proportion to availability, and whether canids switched among alternative prey. This approach tests for joint relationships between variables in particular categories and their interactions (Agresti 1984; Fienberg 1970). Selection of a particular prey type by a predator for a given time period was determined with Manly's alpha selectivity index (Manly et al. 1972):

$$\alpha_i = \frac{r_i/n_i}{\sum_{j=1}^{m} \left(r_j/n_j\right)},$$

where r_i and r_j are numbers of prey types i and j in the diet, n_i and n_j are the numbers of prey types i and j in the environment, and m is the number of potential prey types. This index accounts for relative availability of prey and can include >2 food types. Its values can be compared across different food densities and are scaled from 0 to 1, permitting its use in log-linear model analysis (Heisey 1985). Prey selection is considered random at $\alpha_i = 1/m$ but can be rescaled to an index symmetrical around 0 (Chesson 1983) and satisfies the general criteria for a suitable selectivity index (Cock 1978). Categorical variables for the log-linear analyses were based on either prey numbers or biomass and included a comparison of canid selection of different prey species (prey selection) and comparisons of prey consumptions between pre– and post–ice storm periods (time) and coyotes and red foxes (predator), with prey switching indicated through a significant prey and time interaction. We used traditional model-building techniques (Box et al. 1978), in which resulting nonsignificant higher-order interactions were removed and a reduced model analyzed instead.

We calculated biomass of different prey types consumed per predator per time period by multiplying average prey biomass with percent of a prey type's carcass likely consumed by coyotes and red foxes. Average prey biomasses were obtained from the trap data for mice and voles and from weights reported in the literature for tree and ground squirrels, woodchucks (*Marmota monax*), pheasants, rabbits, and deer (Hoffmeister and Mohr 1972; Kurta 1995; Terres 1995). We assumed that coyotes and red foxes consumed 100% of the carcasses of rabbits and other small mammals (L. A. Randa, pers. obs.; Lockie 1959; Patterson 1995). Canid consumption of a white-tailed deer carcass was estimated to be 80% for coyotes (Patterson et al. 1998; Weaver 1993) and 40% for red foxes (Webbon et al. 2004). All deer remains in scats belonging to a particular predator species that were found during a month's collection period were counted as 1 deer consumed. This was done to account for the large biomass of deer, the small proportion of remains represented in 1 scat (Weaver 1993), and the low probability of locating all scats resulting from consumption of a single deer. Although biases

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exist when estimating frequency of occurrence and amount of biomass consumption from scat data (e.g., small prey may be underrepresented in number but overrepresented in mass [Floyd et al. 1978; Weaver 1993]), we believed that these estimates were useful when limited to relative comparisons of prey consumption by predators in a given area, as in our investigation.

Scat deposition and prey selectivity were not ascertained on an individual basis, raising the concern that prey consumptions reflected the dietary choices of only several individual predators. However, we do estimate that Fermilab could accommodate 2 or 3 fox families, averaging 2 adults and 4 pups each (Allen and Sargeant 1993; Lewis et al. 1993) and at least 1 coyote pack of 5 or 6 adults and 4–7 young (Gehrt 2006).

Lastly, we analyzed age selection of voles by a chi-square test with continuity correction, using SAS PROCEDURE FREQ (SAS Institute Inc. 2007). Significance for all analyses was accepted at $\alpha = 0.05$ and values are reported as means $\pm$ 1 *SE*.

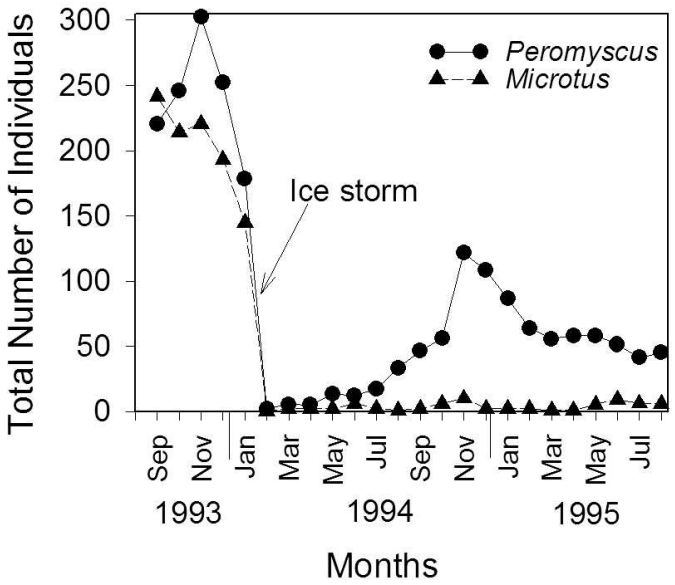


Fig. 1.—Abundances of mice (*Peromyscus*) and voles (*Microtus*) summed across all 21 transects in Fermilab over time.

Results

Prey availability.—We estimated there were 3,697 vertebrate prey available along all 21 transects over the course of the study. Mice were the most abundant prey captured (n = 2,079, 56.2% of total) and included white-footed mice (*P. leucopus*) and deer mice (*P. maniculatus*). Voles were the next most commonly captured prey (n = 1,082; 29.3% of total) and were represented by primarily meadow voles (*M. pennsylvanicus*) but also prairie voles (*M. ochrogaster*). We counted 318 rabbits (eastern cottontails; 8.6% of total), 92 deer (2.5% of total), and 81 pheasants (2.2% of total). For sciurids, we captured eastern chipmunks (*Tamias striatus*) and thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*), and observed fox squirrels (*Sciurus niger*), gray squirrels (*S. carolinensis*), and woodchucks during the visual counts. These 5 sciurids comprised 1.2% of prey (n = 45). We captured only 10 shrews during the entire study, which included northern short-tailed shrews (*Blarina brevicauda*) and masked shrews (*Sorex cinereus*). Vertebrate prey were grouped based on their availability into the categories of mice, voles, rabbits, deer, pheasants, sciurids, and other vertebrates (including shrews).

Most vertebrate prey declined after the January 1994 ice storm, with mice and voles exhibiting the strongest responses (Fig. 1). Before the ice storm, we captured an average of 251.2 $\pm$ 19.0 mice (range = 187–317 individuals) and 174.6 $\pm$ 33.9 voles (range = 77–253 individuals) per month across all 21 transects. Shortly after the ice storm, we observed dead voles lying exposed on the ground. In February 1994, virtually no voles and few mice were captured in the live traps or observed in the field. Vole numbers remained low for the remainder of the study (monthly $\bar{X}$ = 3.7 $\pm$ 0.6, range = 0–10 individuals), whereas mice eventually increased but never reached their former pre–ice storm levels (monthly $\bar{X}$ = 45.7 $\pm$ 7.6, range = 2–113 individuals; Fig. 1). Rabbits showed a moderate decline from their pre–ice storm monthly average of 25.8 $\pm$ 3.9 individuals (range = 12–34) to 10.6 $\pm$ 1.3 individuals (range = 3–26; Fig 2a) after the ice storm. Pheasants declined by 46% (pre–ice storm $\bar{X}$ = 4.6 $\pm$ 0.2, post–ice storm $\bar{X}$ = 3.1 $\pm$ 0.2) and sciurids declined by 34% (pre–ice storm $\bar{X}$ = 3.2 $\pm$ 0.5, post–ice storm $\bar{X}$ = 1.5 $\pm$ 0.1). In contrast, we estimated a 30% increase in deer occupying Fermilab as a whole between the winters of 1993–1994 (n = 380) and 1994–1995 (n = 494) or from 3 to 4 individuals, when adjusted for the area occupied by the 21 transects. We included only mice, voles, and rabbits in the analyses of prey population fluctuations because they were the 3 most common vertebrate prey and constituted 94% of potential prey available.

Abundance of mice, voles, and rabbits differed significantly before the ice storm (species effect: F = 53.28, *d.f.* = 2, 8, P = 0.0001). Because all 3 species had relatively high numbers in November 1993 followed by a decline through January 1994, their abundances did not significantly covary with time (R^2 = 0.969, F = 4.43, *d.f.* = 1, 8, P = 0.0684) nor was the interaction of time and species significant (F = 1.27, *d.f.* = 2, 8, P = 0.3319). After the ice storm, abundance changed significantly over time (R^2 = 0.724, F = 14.84, *d.f.* = 1, 42, P = 0.0004) but did not differ significantly among the 3 prey (species effect: F = 0.43, *d.f.* = 2, 42, P = 0.6549). The greater increase and subsequent decrease in mice as compared to voles and rabbits during the fall of 1994 (Fig. 1) lead to a significant time and species interaction (F = 13.51, *d.f.* = 2, 42, P = 0.0001).

Prey identified in predator scats.—We collected 330 coyote scats (pre–ice storm: n = 65, post–ice storm: n = 265) and 53 red fox scats (pre–ice storm: n = 17, post–ice storm: n = 36) from September 1993 through August 1995. Fewer red fox scats were collected because there were at least one-third as many tracks, on which foxes frequently defecate (Mitchell and Banks 2005), as observed on scat routes and scent stations

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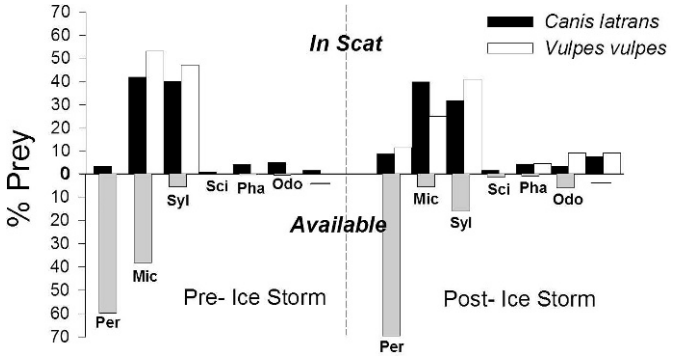


FIG. 2.—Pre– and post–ice storm comparison of number of prey consumed by *Canis latrans* and *Vulpes vulpes* relative to prey available. Prey abbreviations: Per = *Peromyscus*; Mic = *Microtus*; Syl = *Sylvilagus*; Sci = Sciuridae; Pha = *Phasianus*; Odo = *Odocoileus*; — = other vertebrates (data not available for abundance of latter food category).

monitored for a concurrent study (Randa 1996). There also were fewer direct observations of red foxes compared to coyotes, especially after the ice storm (Randa 1996). Mice, voles, and rabbits comprised 80.8% (494 of 612) and 83.6% (51 of 61) of the individual prey items identified in coyote and red fox scats, respectively. Deer, pheasants, sciurids, and other vertebrates (e.g., shrews, passerines, geese, and ducks) comprised 15.8% (n = 97) of coyote diets and 16.4% (n = 10) and of red fox diets (Fig. 2). We found arthropods (insects and occasional crayfish) and plant material (the latter divided into seeds and herbaceous matter, primarily grass) in coyote scats only; each of these constituted <1.5% of food items identified in their scats. Because mice, voles, and rabbits represented the greatest number of prey available to and consumed by coyotes and red foxes, we analyzed predator dietary responses to just these 3 prey as well as these prey plus deer, pheasants, and sciurids.

Number of prey consumed relative to prey available.—The frequency of occurrence of mice, voles, and rabbits in canid diets significantly differed compared to their availability during the entire study period (prey selection; Table 1). A shift by both canids to the most abundant prey, mice, and a disproportionate consumption of voles after the ice storm (Fig. 1) contributed to a significant prey selection and time interaction (Table 1). The similar prey selection and switch to mice by both predators precluded significant predator and time and predator and prey selection interactions (Table 1). After the ice storm, coyotes' consumption of other vertebrates, primarily non–pheasant birds, 6 northern short-tailed shrews, and 1 raccoon (*Procyon lotor*), increased by approximately 6%, whereas red foxes began feeding on deer, pheasants, and other vertebrates (all non–pheasant birds; Fig. 2). This dietary shift represented an approximately 30% increase in mice and other prey although voles were still frequently selected (Fig. 2). When frequency of occurrence of deer, pheasants, and sciurids were incorporated into the log-linear model, there were significant differences in prey types selected overall (prey selection; Table 1) and between the 2 predators (predator; Table 1; Fig. 2), as well as the proportion of prey consumed before and after the ice storm (time; Table 1). Prey switching was still detected (prey selection and time interaction; Table 1) and differed significantly between the predators (predator and time interaction; Table 1), due, in part, to the continued selection of rabbits by red foxes (Fig. 2).

Biomass of prey consumed relative to prey available.—Selectivity index values computed only for biomass consumed of mice, voles, and rabbits were identical to values based on frequency of occurrence and hence also the results for log-linear model analysis. When biomass consumptions of all 6 types of vertebrate prey were included in the log-linear model, there was significantly greater consumption of prey other than deer and mice (prey selection; Fig. 3; Table 1). Biomass consumptions differed between coyotes and red foxes (predator; Table 1) and changed significantly after the ice storm (time and prey selection and time interaction; Table 1). After the ice storm, coyotes showed a 14.5% reduction in deer biomass and a corresponding increase in other prey, namely

TABLE 1.—Results of log-linear analyses for pre– and post–ice storm prey selection by coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*) in relation to prey availability. Highest-order interaction was not significant so reduced models are reported.[a]

Variable	*d.f.*	$\chi_{f.o.}^2$	*P*	χ_b^2	*P*
		Three-prey models			
Prey selection	2	40.38	≤0.0001	40.38	≤0.0001
Time	1	0.70	0.4039	0.70	0.4039
Predator	1	0.10	0.7529	0.10	0.7529
Prey selection × time	2	111.29	≤0.0001	111.29	≤0.0001
Predator × time	1	0.82	0.3651	0.82	0.3651
Predator × prey selection	2	3.04	0.2184	3.04	0.2184
		Six-prey models			
Prey selection	5	40.40	≤0.0001	55.66	≤0.0001
Time	1	1.28	0.2573	0.13	0.7221
Predator	1	8.18	0.0042	6.91	0.0086
Prey selection × time	5	75.01	≤0.0001	99.21	≤0.0001
Predator × time	1	9.17	0.0025	0.00	0.9601
Predator × prey selection	4	8.12	0.0872	2.23	0.6935

[a] $\chi_{f.o.}^2$ = chi-square statistic for frequency of occurrence of prey consumed by predator; χ_b^2 = chi-square statistic for biomass of prey consumed by predator.

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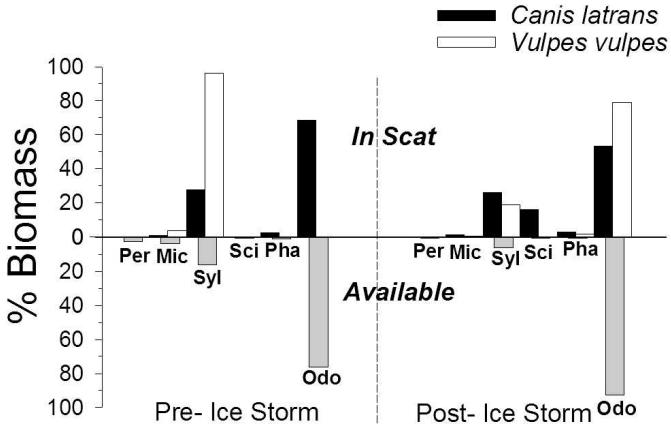


FIG. 3.—Pre– and post–ice storm comparison of biomass of prey consumed by *Canis latrans* and *Vulpes vulpes* relative to prey available. Prey abbreviations: Per = *Peromyscus*; Mic = *Microtus*; Syl = *Sylvilagus*; Sci = Sciuridae; Pha = *Phasianus*; Odo = *Odocoileus*.

sciurids, whereas red foxes switched from obtaining most of their prey biomass from rabbits before the ice storm to include rabbits, pheasants, and deer after the ice storm (Fig. 3).

Seasonal comparison of coyote diets.—The sample size of coyote scats, unlike that of red fox scats, enabled us to perform a categorical analysis of their diets on a seasonal basis. The frequency of occurrence of mice, voles, and rabbits in proportion to their availability differed overall (prey selection; Table 2) with coyotes exhibiting significant dietary switching among these 3 prey over time (prey selection and time interaction; Table 2) but appeared to generally choose voles and rabbits over mice based on alpha index values (Fig. 4). We identified significant switching events from post hoc comparisons of maximum-likelihood estimates corresponding to each prey selection and time interaction category. Of the 3 primary prey, coyotes selected mostly rabbits in fall and winter of year 1 (rabbits: $\chi^2 = 106.09$, $P < 0.0001$; Fig. 4) but selection of voles, in particular, changed significantly in spring of year 1 ($\chi^2 = 102.00$, $P < 0.0001$) after numbers of these prey decreased after the ice storm (Fig. 1). Coyotes increased consumption of mice, still preferentially selected voles, and consumed rabbits more in proportion to their availability (Fig. 4). For year 2, selection of voles and rabbits continued with a compensatory increase of the most numerically abundant prey, mice, during fall, winter, and spring ($\chi^2 = 5.99$, $P = 0.0144$) when rabbit abundance declined (Fig. 4). When frequency of occurrence of deer, pheasants, and sciurids were included in the log-linear analysis, none of the model terms were significant (Table 2). Thus, relatively small shifts to these species masked significant alterations among the 3 main prey appearing in coyote diets.

Seasonal differences in prey biomass selection and results of the log-linear model were identical to the frequency of occurrence of mice, voles, and rabbits. Biomass consumed among the 6 vertebrate prey groups differed significantly (prey selection; Table 2) and among seasons (time, Table 2) but no pronounced switching events were detected (prey selection and time, Table 2).

Coyotes consumed a significantly greater proportion of juvenile voles after the ice storm ($\chi^2 = 11.655$, *d.f.* = 1, $P = 0.0010$). Of 52 individuals for which age could be determined that were collected from coyote scats, 16.0% ($n = 25$) and 66.7% ($n = 27$) were juveniles during pre– and post–ice storm periods, respectively. The post–ice storm period had greater overlap with months of low reproductive activity for voles than the pre–ice storm period.

DISCUSSION

Over the duration of our study, coyotes and red foxes consumed voles, rabbits, and, to a lesser extent, mice more frequently than other prey. Changing abundances of these small mammals over time and the presence of alternative prey provided an impetus for canid dietary shifts and the opportunity to test for switching behavior and differential resource use. A potential confounding factor was that coyotes, in particular, can move across large areas and scats we collected at Fermi could have contained a significant amount of prey from outside its boundaries. However, regional coyotes tend to form small packs of 5 or 6 adults plus young in protected areas (e.g., preserves) within the urban landscape and actively defend territories averaging only 8 km^2 (Gehrt 2006). It is not uncommon that individuals of a pack remain within the boundaries of these large preserves (e.g., >1,000 ha). Red foxes also tend to have more limited movements under higher fox population densities, typical of

TABLE 2.—Results of log-linear analyses for seasonal prey selection by coyotes (*canis latrans*) and red foxes (*Vulpes vulpes*) in relation to prey availability. If highest-order interaction was not significant, reduced model is reported.[a]

Variable	*d.f.*	$\chi_{f.o.}^2$	*P*	χ_b^2	*P*
		Three-prey models			
Prey selection	2	1.66	≤0.0001	41.66	≤0.0001
Time	7	23.01	0.0017	23.01	0.0017
Prey selection × time	13	211.98	≤0.0001	211.98	≤0.0001
		Six-prey models			
Prey selection	5	1.53	0.9091	1,4430.18	≤0.0001
Time	7	0.24	1.0000	2,560.92	≤0.0001

[a] $\chi_{f.o.}^2$ = chi-square statistic for frequency of occurrence of prey consumed by predator; χ_b^2 = chi-square statistic for biomass of prey consumed by predator.

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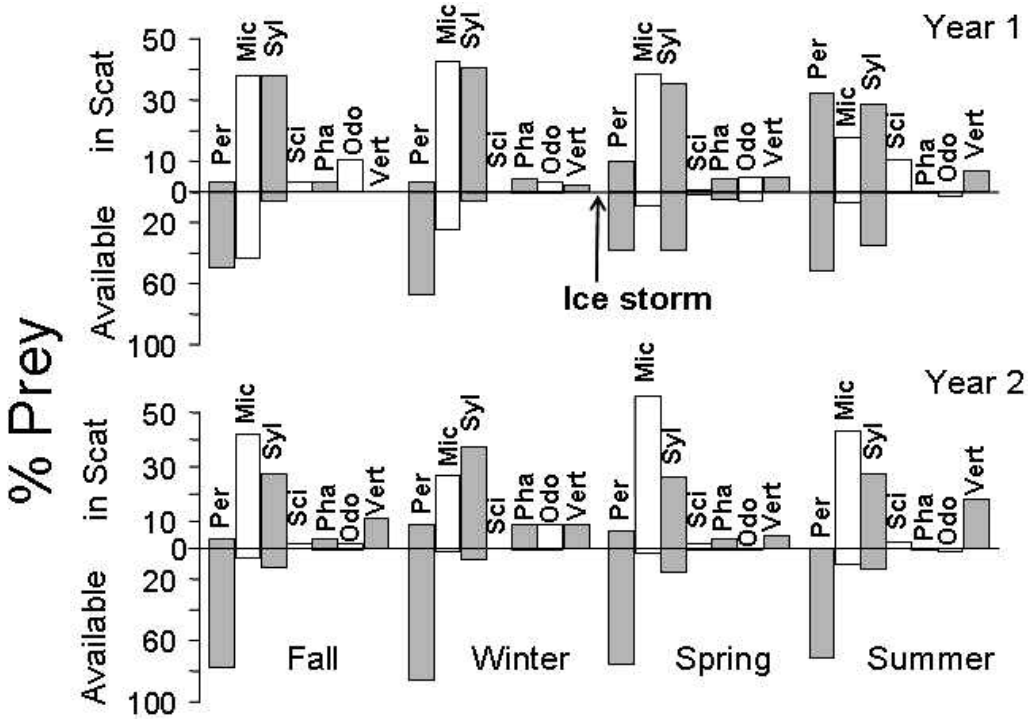


Fig. 4.—Seasonal comparison of number of prey consumed by *Canis latrans* relative to prey available over 2 years (year 1 = 1993–1994, year 2 = 1994–1995). Prey abbreviations: Per = *Peromyscus*; Mic = *Microtus*; Syl = *Sylvilagus*; Sci = Sciuridae; Pha = *Phasianus*; Odo = *Odocoileus*; Vert = other vertebrates (data not available for abundance of latter food category).

urban environments (Gosselink et al. 2003; Trewhella et al. 1988). Fermilab represented a relatively large area (2,800 ha) with abundant refugia for predators and prey amidst a moderate amount of suburban development. Because open spaces like these tend to support resident coyotes and red foxes, we assumed that diets of predators assessed from scat at our site reflected use of prey primarily within our study area.

Diets of coyotes and red foxes differed significantly from one another predominantly because of overall greater diversity of vertebrate prey used by coyotes compared to red foxes. It was not, as we initially hypothesized, simply due to differential selection among primary prey species, that is, mice, voles, and rabbits, when prey were relatively abundant. Before the ice storm, prey of all categories were consumed by coyotes but only voles and rabbits were consumed by red foxes. Our 2nd and 3rd hypotheses were only partially supported in that after the ice storm, both canids continued consuming an unexpected and disproportionately high number of voles and rabbits but showed a small increase in consumption of the more-abundant mice, as well as other prey. Our prediction of different pre– and post–ice storm shifts to alternative prey by coyotes and red foxes was supported when comparing the numbers but not biomass of mice, voles, rabbits, deer, pheasants, and sciurids they consumed.

Although diversity of diets increased between coyotes and red foxes after the ice storm, prey use could have been sufficiently similar to reduce the number or occurrence of red foxes at Fermilab. The paucity of red fox compared to coyote sign in the post–ice storm period may have reflected a decline of red foxes (Roughton and Sweeney 1982; Stoddart 1984). Because canids tend to expand their home ranges when prey availability decreases (Andelt et al. 1987), more coyote–fox encounters would likely result in the displacement of red foxes by coyotes (Gese et al. 1996b; Sargeant and Allen 1989). In a comparable example, diverse but significantly similar diets between sympatric coyotes and red foxes in southern Illinois apparently contributed to a decline in red foxes when coyote numbers increased (Cypher 1993).

The seasonal dietary analyses for coyotes also demonstrated that voles and rabbits were generally the most frequently consumed prey each season, with selection for voles actually increasing after their decline in abundance. A notable switch to consuming mice more than other prey temporarily occurred after a protracted period of very low vole abundance. Great horned owls (*Bubo virginianus*) studied in conjunction with the canids at Fermilab also tended to select voles over other prey (Cooper 1997). It is possible our measure of prey selection based on relative prey abundance did not accurately reflect prey choice by canids. Other studies have demonstrated that prey choice of coyotes (Prugh 2005; Windberg and Mitchell 1990) and red foxes (Leckie et al. 1998) can be driven by absolute rather than relative abundance of the selected prey. Coyote depredation of common alternative prey may be impeded if that prey occupies a habitat different from more frequently selected prey (Prugh 2005). This was partially true in our study in which one of the most common alternative prey, mice, was found in many of the same habitats as the most frequently selected prey, voles and rabbits, as well as in woodlands that were not used by coyotes (Randa and Yunger 2004).

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Age selection of prey may explain how predators in our study continued to consume voles in disproportionately high numbers, when monthly trap surveys indicated that their numbers were extremely low. Few adult voles remained after the ice storm, which occurred during the voles' nonreproductive period. Conservative age estimates of arvicoline remains in scat indicated that coyotes shifted from consuming a greater proportion of older voles to very young voles after the ice storm; great horned owls at Fermilab exhibited a similar behavioral response (Cooper 1997). These findings, coupled with our low capture rates of voles after the ice storm, suggest that predators apparently consumed juvenile voles before they entered the trappable population (i.e., became territorial individuals or dispersers). By finding and consuming young voles before they reached a reproductively active age, predators helped inhibit recruitment, thereby prolonging or exacerbating the low-density period for vole populations. The significant role predators had in limiting vole populations was experimentally supported at our study site (Yunger 1996) and is similar to the effect predators have had on other arvicoline populations in North America (Reid et al. 1995).

Despite the high number of voles that consistently appeared in coyote diets, deer or rabbits accounted for the greatest biomass of prey consumed across all seasons. Coyotes likely consumed deer as carrion rather than depredated fawns, because most fawns in our region are born during early summer (Gladfelter 1984) when deer remains did not appear in coyote scats. Ungulate carrion is consumed by both coyotes and red foxes (Gese et al. 1996a; Jędrzejewski and Jędrzejewska 1993) and has been shown to be an important food source for red foxes during winter, especially when adult deer are regularly killed by larger predators (Selva et al. 2005). Although we were unable to assess whether deer were depredated by coyotes, deer remains only appeared in red fox scats in the spring after the ice storm and subsequent winter, further suggesting that depredation of fawns was not an important source of deer biomass for either predator.

If coyotes and red foxes were optimizing their foraging strategy (MacArthur and Pianka 1966), they would have compromised between choosing prey requiring the least amount of energy to procure, through both search and handling effort, and prey yielding the greatest energy gain per unit, that is, the most profitable prey (e.g., Hayward et al. 2006). This approach may have contributed to times of high biomass consumption of rabbits especially if they yielded more energy for a canid due to prohibitive amounts of energy needed to find and capture an equivalent number of voles, kill deer, or find deer carcasses. Alternatively, if coyotes and red foxes foraged strictly opportunistically, they simply would have depredated the most readily encountered prey (e.g., Dell'Arte et al. 2007). This would account for greater vole consumption when they are relatively abundant, but does not sufficiently explain selection of voles during periods of low abundance. These predators possibly learned to search intensively for voles when they were highly abundant and increasingly supplemented their energetic needs with other prey as voles became scarce. In this sense, coyotes and red foxes may have acted more as facultative strategists (Glasser 1984), especially because they are capable of exploiting different prey in different habitats along the urban–rural interface (Randa and Yunger 2004, 2006).

A combination of prey selectivity and switching may reflect the most efficient means of foraging for coyotes and red foxes. They can accomplish this by choosing prey that have more energy per unit mass, are more abundant and readily encountered, or are smaller and easier to handle. Different prey switching strategies likely facilitate coexistence of coyotes and red foxes. However, large-scale declines in primary prey could negatively impact red foxes at the urban–rural interface, and these foxes may face increasing competitive pressure from coyotes amid limited suitable habitat.

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