ABSTRACT

Name: Lynda A. Randa

Department: Biological Sciences

Title: Prey Selectivity and Foraging Activity of *Canis latrans* and *Vulpes vulpes* in Response to Prey Fluctuations and Habitat in a Heterogeneous Landscape

Major: Biological Sciences

Degree: Master of Science

Approved by:

Date:

Thesis Director

27 May 1996.

NORTHERN ILLINOIS UNIVERSITY

ABSTRACT

Predators may forage in a variety of ways, such as specializing on particular prey species, switching to alternative prey, or by varying spatial activity patterns. The latter two modes can occur in a heterogeneous landscape. The effects of fluctuating prey numbers on the activity patterns and diet selection of two terrestrial predators, the coyote (*Canis latrans*) and red fox (*Vulpes vulpes*), were investigated. The study site was located in northern Illinois, at Fermi National accelerator Laboratory (Fermilab), and included sampling in seven different habitats of a heterogeneous landscape. Availability of small mammalian prey was assessed by monthly mark-recapture sampling conducted along three 200-m transects in each of the seven locations. Availability of squirrels (*Sciurus* spp.), eastern cottontail rabbits (*Sylvilagus floridanus*), and Ring-necked Pheasants (*Phasianus colchicus*) was assessed by monthly visual counts along the same transects. Spatial activity patterns of *C. latrans* were determined from scent station lines parallel to the small mammal trapping transects. Scats collected along standardized routes were analyzed for number and occurrence of prey items. During 1994, there were significant differences in prey availability over time between the seven locations. Dietary analyses indicated that both red fox and coyote switched between alternative prey, albeit with a strong preference for *Microtus*. A concurrent study on small mammal population dynamics, conducted in one of the seven habitats, showed experimentally that the preferential selection of voles depressed prey populations. Except for *Microtus*, overall prey availability did

not affect coyote activity patterns across Fermilab. This lack of correlation was due, in part, to habitat selection by coyotes, primarily, the avoidance of wooded areas. Coyotes did, however, respond to abundant patches of *Peromyscus*, through spatial and temporal alterations in activity patterns.

NORTHERN ILLINOIS UNIVERSITY

PREY SELECTIVITY AND FORAGING ACTIVITY OF *CANIS LATRANS* AND *VULPES VULPES* IN RESPONSE TO PREY FLUCTUATIONS AND HABITAT IN A HETEROGENEOUS LANDSCAPE

A THESIS SUBMITTED TO THE GRADUATE SCHOOL IN PARTIAL

FULFILLMENT OF THE REQUIREMENTS

FOR THE DEGREE

MASTER OF SCIENCE

DEPARTMENT OF BIOLOGICAL SCIENCES

BY

LYNDA A. RANDA

DEKALB, ILLINOIS

MAY 1996

Certification: In accordance with department and Graduate School policies, this thesis is accepted in partial fulfillment of degree requirements

Thesis Advisor

27 May 1996.

Date

ACKNOWLEDGMENTS

Many thanks to my advisor, Dr. Peter Meserve, for his counsel and support during my graduate studies. I am also grateful to my committee members, Drs. Sam Scheiner and Carl von Ende, for statistical advise. Special recognition goes to John Yunger whose insight and guidance provided the basis for this study. Doug Cooper shared in much of the field activity. Dr. Rod Walton oversaw Fermilab activities associated with this project and helped obtain funding. Funding for this study was provided by the National Environmental Research Park of the U.S. Department of Energy, and the Department of Biological Sciences, Northern Illinois University.

DEDICATION

I dedicate this work to my children, Christine and Kenny

TABLE OF CONTENTS

	Page
LIST OF TABLES	vi
LIST OF FIGURES	viii
INTRODUCTION	1
STUDY SITE AND METHODS	11
RESULTS	29
DISCUSSION	56
LITERATURE CITED	67

LIST OF TABLES

Table		Page
1.	Pre-Ice Storm Covariate Analysis of Minimum Number Known Alive for the Three Main Prey Species Across All Seven Sampling Locations; $R^2 = 0.9686$	31
2.	Post-Ice Storm Covariate Analysis of Minimum Number Known Alive for the Three Main Prey Species Across All Seven Sampling Locations; $R^2 = 0.7245$	32
3.	Coyote and Red Fox Diet Selection Prior to and Following the Ice Storm	36
4.	Coyote Diet Selection of Different Prey Species Over Time	39
5.	Maximum Likelihood Parameter Estimates	40
6.	Age Selection of Voles by Coyotes During Pre- and Post-Ice Storm	42
7.	Results of Covariate Analysis of Minimum Number Known Alive for the Three Main Prey Among Seven Locations; $R^2 = 0.6581$	46
8.	Results of Multiple Regression Analysis of Coyote Activity vs. Abundance of Prey Species and Habitat Variables; $R^2 = 0.2647$	50
9.	Results of Repeated Measures Analysis of Variance for Coyote Activity Around Food Supplemented vs. Not Supplemented Plots	53

10. Results of Regression Analysis of *Canis latrans* Activity With a One-Month Time Lag vs. Abundance of *Peromyscus* squared ; $R^2 = 0.6245$ 54

LIST OF FIGURES

Figure		Page
1.	Map of Fermilab showing the seven different study locations	16
2.	Map of experimental plots at Tallgrass Prairie II, showing predator exclusion and predator access plots, and plots in which the food supplementation experiment was conducted	21
3.	Average abundances of the three main prey of canids over time across all seven sampling locations	30
4.	Pre- and post-ice storm comparison of prey consumed by *Canis latrans* and *Vulpes vulpes* vs. prey available. Per = *Peromyscus*; Mic= *Microtus*; Syl=*Sylvilagus*; Sci=Sciuridae; Pha =*Phasianus*; Odo=*Odocoileus*; Vert=Other Vertebrates; Invert=Invertebrates; Seed=Seeds; Herb=Herbaceous material	34
5.	Seasonal comparison of prey consumed by *Canis latrans* vs. prey available. Per = *Peromyscus*; Mic=*Microtus*; Syl=*Sylvilagus*; Sci=Sciuridae; Pha=*Phasianus*; Odo=*Odocoileus*; Vert=Other Vertebrates; Invert=Invertebrates; Seed=Seeds; Herb=Herbaceous material	38
6.	Activities of *Canis latrans* over time between the seven habitats	43
7.	Abundances of the three main prey in each of the seven habitats over time	45
8.	Activities of *Canis latrans* vs. abundances of each of the three main prey	48

9. Activities of *Canis latrans* vs. each of the three vegetation variables 49

10. Activities of *Canis latrans* on food-supplemented vs. not supplemented plots 52

11. Activities of *Canis latrans* with a one-month time lag, in Oakwoods I vs. abundance of *Peromyscus* 55

INTRODUCTION

Resource availability can affect predators in a variety of ways. For example, variations in prey abundance may elicit numerical or behavioral responses of the predator. Prey populations may exhibit substantial annual (Howell 1923, Finerty 1980, Akçakaya 1992) or seasonal fluctuations (Krebs 1966, Krebs et al. 1969, Getz et al. 1979, Baker 1983, Meserve and Klatt 1985, Getz et al. 1987, Hoffmeister 1989, Schramm and Willcutts 1983, Yunger 1996) resulting in temporal changes in their availability. Variable prey abundance could also be due to spatial partitioning of prey in heterogeneous environments. That is, different prey may be located within particular habitats in a heterogeneous landscape or a species' abundance may vary between different habitats. Additionally, prey may be patchily distributed within a particular habitat.

The numerical responses of vertebrate predators elicited by these differential prey densities are simply a change in the number of predators in a given area (e.g., Jaksic et al. 1992, Breitenmoser and Haller 1993, Jaksic et al. 1993, Holt et al. 1994, Neimuth and Boyce 1995). These numerical responses are often directly correlated with the availability of prey. For example, predators may respond positively to increased prey abundance by increased immigration and/or reproduction and survivorship (Elton 1942, Solomon 1949, Beddington et al. 1976, Harris and Bowman 1980). When prey abundance decreases, predators may emigrate, reproduce less, and/or die. Work by Korpimäki and Norrdahl

(1991) and Korpimäki (1994) in southern Scandinavia demonstrated that Eurasian Kestrels (*Falco tinnunculus*) and Short-eared Owls (*Asio flammeus*) responded numerically to fluctuations of prey species by migrating. This tracking of prey populations across the landscape resulted from responses to prey densities located within particular areas of the landscape. Less vagile predators may alter their reproductive output in response to changing prey availability. Numerical responses due to decreased reproduction during a decline in primary prey species have been documented for both red foxes (*Vulpes vulpes*) in Alaska (Zabel and Taggart 1989) and kit foxes (*Vulpes velox*) in the western United States (Egoscue 1975). Long-term numerical responses have been demonstrated by northern populations of coyotes (*Canis latrans*), whose cyclic fluctuations have been directly correlated with the ten-year cycle of snowshoe hares, *Lepus americanus* (Keith 1963, Todd et al. 1981). Similar numerical responses have been described for coyotes to black-tailed jack rabbits (*Lepus californicus*) in the Great Basin area of the U. S. (Clark 1972).

In addition to numerical responses, predators may respond behaviorally to changes in prey abundance through functional responses. The functional response is defined as the number of prey consumed per unit time by a predator, which is a function of prey density (Holling 1959). Initially, most functional response studies were conducted on invertebrates under controlled laboratory conditions (e.g., Holling 1966, Messenger 1968, Griffiths 1969, Murdoch and Oaten 1975, Oaten and Murdoch 1975, Hassell 1978) using a simple one predator-one prey system with variations in the temporal or spatial

availability of prey. For example, Landenberger (cited in Murdoch and Oaten 1975) continually replaced turban snails, *Tegula*, to observe a starfish's, *Pisaster*, response to the rate at which the prey were made available. Alternatively, Hassell (1971) differentially distributed almond moth larvae, *Ephestia*, between various patches to observe predation by the parasite *Nemeritus*. Murdoch (1969) expanded the study of functional responses to a one predator-two prey system in which snails, *Acanthina*, the predator, were simultaneously presented with a mussel, *Mytilus edulis*, and a barnacle, *Balanus glandula*, both in the laboratory and in the field. More recently, functional response studies have been applied to vertebrates (e.g., Lundberg 1988, Jaksic et al. 1992, Fryxell and Doucet 1993, Soluk 1993, Dale et al. 1994, Piersma et al. 1995). Among vertebrate predators, a type III functional response was considered to be most common, due either to development of a search image or switching to alternative prey (Murdoch and Oaten 1975). However, the functional response curves of terrestrial and avian vertebrate predators' foraging behavior have not been as clearly defined as those of invertebrates. This can be attributed to the greater difficulty of working with vertebrate predators in controlled situations, and hence, by relatively fewer studies of vertebrate predator functional responses.

Switching behavior is a particular expression of the functional response and of diet selection. Switching, the disproportionately greater consumption of the more relatively abundant prey species, was first defined by Murdoch (1969). However, the occurrence of switching was described even earlier by Cabot (1920), who noted that arctic predators

apparently turned to consuming ptarmigan when the abundance of mice suddenly decreased. There are numerous experimental studies on the switching behavior of invertebrates (e.g., Clarke 1962, Murdoch 1969, Murdoch and Marks 1973, Lawton et al. 1974, Cornell 1976, Akre and Johnson 1979) as well as vertebrates (e.g., Murton 1971, Manly et al. 1972, Murdoch et al. 1975, Hughes and Croy 1993), carried out under highly controlled conditions. Investigations of invertebrate switching behavior stemmed largely from functional response studies of one predator-two prey systems, as in Murdoch's (1969) seminal work. In initial switching studies, the prey species were distributed close together, but later work focused on locating different prey in patches. For vertebrates in particular, it was found that spatial variability of prey, or the occurrence of different prey across patches was one mechanism inducing predator switching behavior (Murdoch and Oaten 1975, Murdoch et al. 1975). In addition to spatial variability of prey, temporal fluctuations of prey populations can also cause predator switching behavior. Regional vertebrate prey populations of temperate North America illustrate the occurrence of such fluctuations in population density. For example, arvicoline (i.e., voles and lemmings) densities may fluctuate by an order of magnitude within a one-year period (Krebs et al. 1969, Getz et al. 1979, Getz et al. 1987). Eastern cottontail rabbits, *Sylvilagus floridanus*, can also have substantial (though less dramatic) within-year fluctuations (Lord 1958) and local populations of mice, *Peromyscus* spp., are known to vary seasonally (Yunger 1996, Wolff 1996). These small mammal populations can also show even more

dramatic between-year differences in numbers, unrelated to a cyclic phenomenon (Meserve and Klatt 1985, Getz 1979, Getz et al. 1987, Hoffmeister 1989).

In general, there has been a lack of switching studies conducted on natural populations of vertebrate predators and their prey. A notable exception is work by Erlinge et al. (1983) and Erlinge (1987) in Scandinavia, who demonstrated the importance of switching behavior in vertebrate predator-prey systems. They found that generalist predators (such as the red fox and the polecat, *Mustela putorius*) switched between alternative small mammal prey, thereby maintaining the noncyclic pattern of the prey populations. However, the switching behavior enabled predators to reach higher densities as compared to more northern Scandanavian regions, thereby helping to maintain stable predator populations. In turn, the number of predators was probably limited by territorial behavior, which, overall, further helped to stabilize this predator-prey system.

In a comparison of studies of vertebrate predators and mammalian prey, Jaksic et al. (1993) noted that numerical responses and behavioral responses (specifically, functional responses) can be "uncoupled components of vertebrate predation." That is, either one, both, or neither one of these responses may be exhibited by predators to changing prey abundances in a given system. Thus, although they are not necessarily mutually exclusive, it is possible to focus on one type of predator response without it being confounded by the other. The advantage of focusing on one response may depend on the time frame in which the study is being conducted (e.g., behavioral responses can occur in a much shorter time frame than numerical ones).

The spatial activity patterns of vertebrate predators are closely coupled with their foraging behavior. It is well recognized that the behavior, distribution, and spatial organization of predators is largely related to resource availability (e.g., see Macdonald 1983, and Bekoff et al. 1984 for a review of carnivores). The adaptability of the predator's behavioral responses indicates its ability to respond spatially to its prey. Some members of the family Canidae in particular, exhibit a high degree of intraspecific variation in diet composition, and spacing systems due to spatial and temporal patterning of food resources (Moehlman 1989). These variations may occur within or between populations and vary seasonally or between years. For example, spacing of red foxes has been correlated with availability and dispersion of food (Macdonald 1981, Lovari et al. 1994, Poulle et al. 1994, Catling and Burt 1995). Likewise, coyote (Shivik and Crabtree 1995) and wolf (Larter et al. 1994, Sillerozubiri and Gottelli 1995, Sillerozubiri et al. 1995) activities can vary seasonally based upon prey availability (e.g., Messier [1985] found that wolves responded to a decrease in food availability by increasing their spatial distribution). The amount of time a predator allocates to foraging activities also influences its spatial activity patterns. Although movements and activity patterns have been explicitly described for some vertebrate predators (e.g., Andelt and Gipson 1979, Holzman et al. 1992), there has often been, at best, only circumstantial evidence as to the cause (e.g., Person and Hirth 1991). The temporal activity patterns of canids tend to vary in response to those of their prey (Sheldon 1992). Thus, generalist canid predators could be expected not only to alter their diets in response to changes in prey but their spatial activity patterns as well.

Variations in habitat can also influence the movements and activities of predators (Clark et al. 1993, Lamberson et al. 1994). Habitat differences may even constrain behavioral responses of predators. That is, predators may selectively utilize and/or avoid particular habitat types (DeJong 1995, Smallwood 1995). As a result, predators may not respond to changes in prey availability within certain habitats. This habitat selectivity may be quantified through broad habitat measures such as foliage density, canopy coverage, and ground coverage. However, these vegetation measures may also be related to or reflect prey usage (e.g., Anthony et al. 1981). Such inter-relatedness must be considered when making inferences of predator behavior.

Recently, attention has focused on the importance of accounting for spatial aspects in ecological investigations (Kareiva 1994). Acknowledging spatial effects is particularly applicable to vertebrate predator-prey studies conducted in heterogeneous landscapes. In particular, vertebrate predators often move over large spatial scales, whereas their smaller prey tend to be more localized (i.e., in different habitats or patches within a habitat). Therefore, it is important to relate predator foraging behavior at a landscape scale to prey abundances within habitats. However, previous studies on vertebrate predators have made inferences of their foraging behavior without accounting for the importance of spatial scale (e.g., Korschgen and Stuart 1972, Hamlin et al. 1984, Jaksic et al. 1993). This has been the result of prey sampling in only one or a limited number of locations utilized by the predators (for exceptions, see Dunk and Cooper 1994, Korpimäki 1994).

Differences in scale may influence how we model and interpret predator-prey interactions (Hanski 1991) and foraging strategies (Ward and Saltz 1994). For example, the spatial patterns utilized by predators can be observed across different scales. These correspond to varying levels of organization such as home ranges and territories within a landscape (e.g., Korpimäki 1994), movements between habitats within that home range or territory (e.g., Todd et al. 1981), and movements between patches within a particular habitat (e.g., Geffen and Macdonald 1993). Furthermore, as previously discussed, the distributions and abundances of prey often vary at different spatial scales (Storch 1993, Brown 1995), especially in fragmented landscapes (Gustafson et al. 1994, Warner 1994, Best et al. 1995). Hence, predator foraging patterns in response to prey availability could be expected to vary depending on the observed spatial scale. For example, a response that appears to be numerical on a local/habitat scale (due to immigration or emigration), could be interpreted as a behavioral response on a landscape scale (due to differential foraging activities).

Although monitoring of predators and prey across different spatial scales may be useful in itself, manipulations of prey populations can reveal underlying mechanisms of predator behavior, and can elicit rapid behavioral responses of predators. Yet, removing or introducing whole prey populations in conjunction with the large spatial scales utilized by vertebrate predators presents both logistical and ethical problems. On the other hand, natural perturbations to systems offer the opportunity to observe comparative effects, often on a larger spatial scale (i.e., landscape scale) than manipulative field experiments

and perhaps with a greater degree of generality (Diamond 1986). Dramatic increases or decreases in prey population numbers due to a variety of abiotic and biotic factors such as drought, storms, fire, or sudden increases in food supply are ways in which a large scale "natural experiment" may occur. Furthermore, large-scale natural disturbances can cause changes in the distribution or species composition of prey (Sale 1977, Connell 1978, Huston 1979, Reice 1985, Hughes 1994). In addition, deliberate habitat manipulations such as burning or mowing result in large-scale perturbations that can elicit such changes in prey populations.

The area in which this study was conducted provided the conditions necessary for detecting predator behavioral responses such as switching and alteration of movements and activities; that is, a heterogeneous landscape with a diversity of spatially and temporally variable prey species, and generalist canid predators (i.e., coyotes and red foxes). Previous studies have shown that coyote (Todd et. al 1981, Andelt et al. 1987, Brillhart and Kaufman 1995) and red fox (Dearborn 1932, Cook and Hamilton 1944, Scott and Klimstra 1955, Jedrzejewski and Jedrzejewska 1993, Patalano and Lovari 1993, Johnson and Franklin 1994, Lucherini and Crema 1994) diets vary seasonally. The purpose of this study was to investigate the effects of spatial and temporal partitioning of prey and habitat differences on the foraging behavior of canids in a heterogeneous landscape. Specifically, data collected on prey abundance, habitat variables, canid diets, and canid activities were used to address the following questions:

1) Do the diets of sympatric red fox and coyote differ significantly?

2) Are the canids switching between alternative prey, in response to changes in prey availability (i.e., do they feed on the most abundant prey)?

3) Do activity patterns of canids vary (a) on a landscape scale (i.e., between habitats) and (b) within a particular habitat in response to changes in prey availability?

4) Do variations in habitat influence the activity patterns of canids?

This study was conducted with concurrent studies on the effects of predation, competition, and food on small mammal population dynamics (Yunger 1996) and the effect of prey availability on raptor diets and activities (Cooper, unpublished data).

STUDY SITE AND METHODS

The System

Study Site

The study site was located in northern Illinois at Fermi National Accelerator Laboratory (Fermilab) in Batavia, Illinois. Fermilab encompasses approximately 3,200 ha and may be characterized as a heterogeneous landscape. The study was conducted at seven different locations within Fermilab, representing five different habitat types. These different habitats were chosen since they included prey species characteristic of coyote and red fox diets. The five habitat types represented were: 1) an oldfield grassland dominated by goldenrod (*Solidago altissima*, *S. canadensis*) and Queen Anne's lace (*Daucus carota*); 2) two tallgrass prairie restorations, one dominated by big bluestem (*Andropogon gerardii*) and the other dominated by tall goldenrod (*S. altissima*) and big bluestem (*A. gerardii*); 3) a non-native grass field (*Bromus* spp. and bluegrass, *Poa*); 4) two oakwoods, one dominated by bur oak (*Quercus macrocarpa*), the other dominated by black oak (*Quercus velutina*); 5) a shrubby oldfield containing a heterogeneous mix of gray dogwood (*Cornus racemosa*), goldenrod (*Solidago* spp.), quaking aspen (*Populus tremuloides*), and a variety of non-native grasses (Byre 1989, personal observation).

Predators

A major portion of Fermilab's approximately 3,200 hectares is comprised of open land such as agricultural fields, oldfields, prairie, and non-native grasslands, habitats which are frequently utilized by coyotes and red foxes in the Midwest. Initial sightings and preliminary observations of scats and tracks in the spring of 1993 indicated that these two canid species were relatively abundant at the site.

Coyote

The coyote is found throughout Illinois, but is not common to any particular area. The coyotes of the northern part of Illinois belong to the subspecies *Canis latrans thammnos* Jackson (Hoffmeister 1989, Hall 1981). Clearing of forests by humans for agriculture and settlement may have provided more suitable habitat for the coyote and enabled it to increase its range in the state. Its preferred habitat is prairie, open grassy fields, and lowland brush (Dice 1925, Mumford and Whitaker 1982). Coyotes tend to hunt on and use woodland edges of open areas (Ozoga and Harger 1966, Litvaitis and Shaw 1980). They have been described as being mainly nocturnal (Mumford and Whitaker 1982) or crepuscular (Baker 1983), but were also seen active during the daytime (personal observation). Andelt and Gipson (1979) found that home ranges of coyotes in Nebraska varied seasonally among some individuals. Their results demonstrated a positive relationship between coyote group size and home range size.

Coyotes have been considered generalist predators (Murie 1940, Korschgen 1957, MacCracken 1984). Previous work has shown that mammals, particularly small mammals, comprise a major proportion of coyote diets (Phillips and Hubert 1980, Cypher et al. 1993). Some reported percentages of food items in the diets of coyotes are: the western U.S.--mammals 93% (51% lagomorphs and rodents, 25% carrion), birds 3%, insects 1%, plants 2%, other animal matter 1% (Sperry 1941); southwestern U.S. (Texas)--mammals 64%, birds 1%, insects 10%, fruits 20%, miscellaneous 5% (Andelt et al. 1987); central U.S. (southwest Oklahoma)--rodents 53%, fruits and seeds 32% (highest in fall, lowest in winter), deer 20%, insects 19.5, birds (and some eggs) 19%, lagomorphs 11%, armadillo 9%, cattle 6%, reptiles 4% (Litvaitis and Shaw 1980); southern Illinois--mammals 87.7%, birds 3.4%, invertebrates (trace), undetermined animal matter 8.0%, plant foods 1.2%, miscellaneous (trace) (Phillips and Hubert 1980). Although previous investigators concluded that coyotes are generalist predators, there is a clear trend towards feeding on mammals.

Red Fox

The red fox is found throughout Illinois and, like the coyote, has probably benefited from humans clearing forests and cultivating the land. Preferred red fox habitats are cultivated and fallow fields, fence rows, along creek banks, lake shores, and other open areas with some cover (Layne and McKeon 1956, Klett et al. 1988, Cavallini and Lovari 1994, Lucherini et al. 1995).

Home ranges of foxes may be influenced by the presence of coyotes. Sympatric coyotes and red foxes tend to have non-overlapping home ranges (Voight and Earle 1983, Harrison et al. 1989, Sargeant and Allen 1989) and fox families may occupy territories approximately five times smaller than sympatric coyotes (Sargeant et al. 1987). Displacement or exclusion of red fox by coyote occurs through the latter's aggression towards foxes and in the subsequent avoidance of coyotes (Dekker 1989, Sargeant et al. 1987, Sargeant and Allen 1989).

As with coyotes, red foxes are considered generalist predators that are more highly omnivorous than coyotes (Errington 1935, Scott 1943, Schueler 1951, Arnold 1956, Ozoga et al. 1982, Lucherini and Crema 1994). Percentages of food items in the diet based on volume of stomach contents from foxes in southern Illinois (Knable 1970) are: mammals 67.1%, birds 10.3%, reptiles 0.3%, invertebrates 2.9%, plants 18.6%, miscellaneous 0.8%. Korschgen (1959) conducted a more detailed study of red fox stomach contents from Missouri and found the following prey items: rabbits 36.8%, mice and rats 13.5%, poultry 13.7%, other mammals 7.7%, carrion 7.7%, livestock 5.1%, birds 3.4%, invertebrates 0.7%, undetermined animal matter 0.1%, plant foods 2.7%, and trace amounts of fish, reptiles, and miscellaneous (non-food) items.

Methods

Availability of Prey

To assess the availability of prey, between September 1993 and March 1994, prey sampling was conducted within a single study location, Tallgrass Prairie II (Fig. 1). Based upon visual observations, snow tracking, and sample trapping at the time, prey abundances at this habitat appeared comparable to other locations across Fermilab.

In March 1994, following a dramatic decline in prey numbers (see Results), sampling was initiated at six additional locations, to ensure that the prey sampling was representative of all prey available. Sampling was conducted along three 200-m transects which were approximately centered in each of the seven habitats (Fig. 1). The transects were parallel and spaced 70 to 85 m apart, depending upon the size of the particular habitat. The minimum distance was chosen to ensure relative independence of transects, at least in relation to small mammals such as mice and voles. Seventeen trap stations were spaced at 12-m intervals along each transect, totaling 51 trap stations per habitat. Trapping was conducted on a monthly basis, two nights in each habitat. One 23 x 9 x 7.5 cm Sherman live-trap, baited with a peanut butter and oats mixture, was placed at each station. Traps were checked early morning and late afternoon (ca. every 12 hr). Small mammals were marked with a uniquely numbered eartag (Monel No. 1, National Band and Tag Co., Memphis, Tennessee). Data on date, trap location, tag number, species, sex, age, weight, and reproductive condition was recorded for each capture.

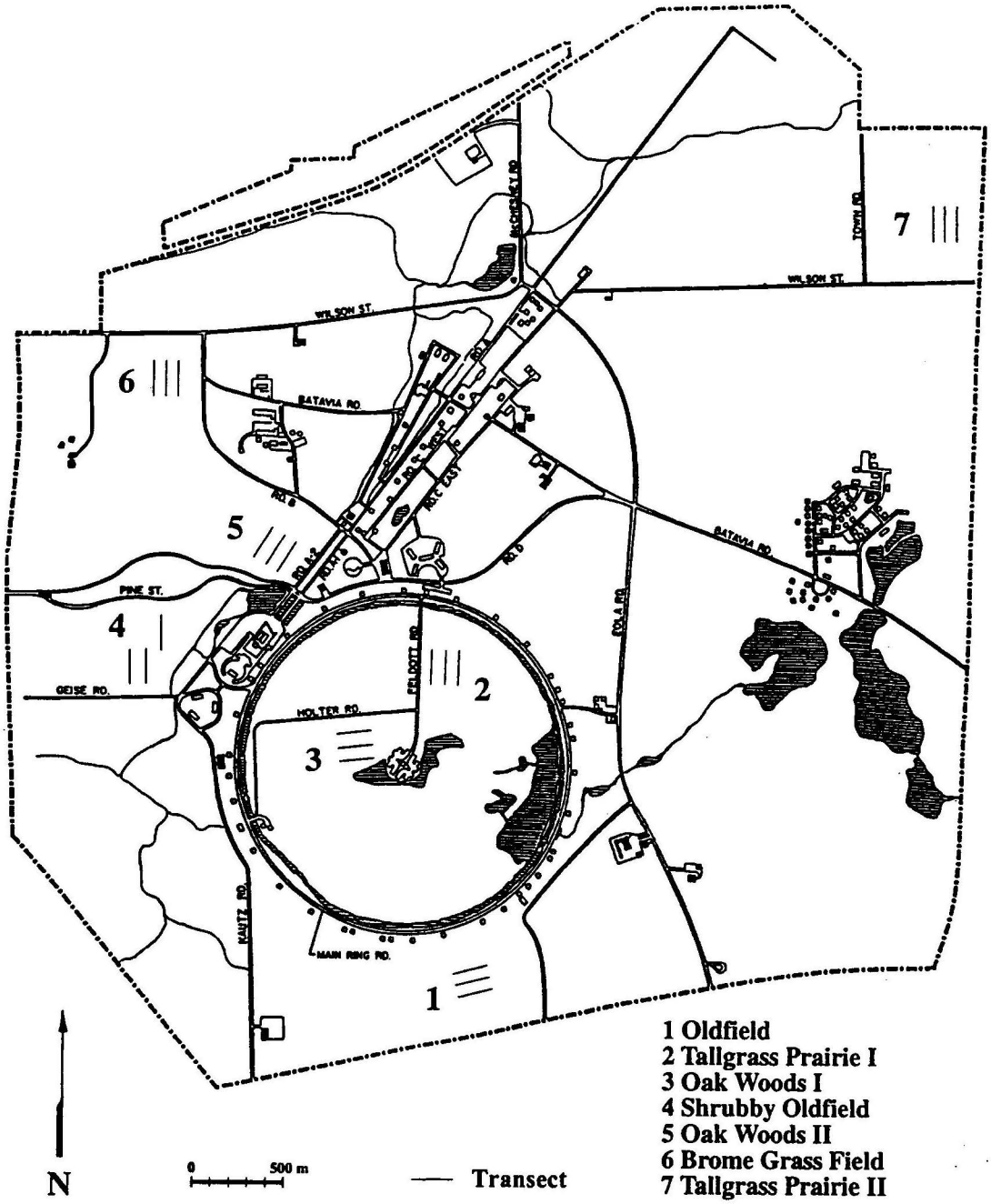

Figure 1. Map of Fermilab showing the seven different study locations.

Monthly diurnal visual counts were used to assess the abundance of Ring-necked Pheasants, *Phasianus colchicus*, and sciurids (fox squirrel, *Sciurus niger*, gray squirrel, *Sciurus carolinensis*, eastern chipmunk, *Tamias striatus*, thirteen-lined ground squirrel, *Spermophilus tridecemlineatus*, woodchuck, *Marmota monax*) in each of the seven study locations. The visual counts were conducted twice during the small mammal trap sessions, by sighting with binoculars along the small mammal trapping transects. Nocturnal visual counts, using a high-powered spotlight (Woolf et al. 1993), were conducted for rabbits in a similar manner to the diurnal visual counts. For the visual counts, the transects were lengthened to 250 m to account for the larger spatial movements of pheasants and rabbits. Estimates of white-tailed deer, *Odocoileus virginianus*, abundance were obtained by a helicopter survey conducted during Winter 1994. The aerial count was conducted with two observers in the helicopter, which traversed the entire lab along a series of parallel transects.

In addition to observing changes in prey availability due to natural fluctuations, fire was used as an indirect means of manipulating prey. Tallgrass Prairie I was burned between the October and November 1994 small mammal surveys. This site was adjacent to Oak Woods I (Fig. 1), which concurrently experienced a high acorn production year. Both habitats contained two closely related species of small mammals (*Peromyscus maniculatus* in the prairie and *P. leucopus* in the woods), which were similar in body size and morphology. Numerical responses, caused by immigration of *Peromyscus maniculatus* to prairie burns have been previously documented (Cook 1959, Kaufman et al. 1983,

Kaufman et al. 1988). Similarly, acorns have been shown to be an important local food source for *Peromyscus* (Ostfeld, et al. 1996; Wolff, in press). Consequently, the localized, substantial increase in the numbers of these two similar species between two different habitats in the same proximity provided the opportunity to observe changes in coyote foraging activity, following natural and experimental manipulations of prey. For example, canids could respond to the increased numbers of these species by increased activity in the general vicinity. Alternatively, canids could show increased activity in only one of the habitats due to specific habitat utilization behavior.

Diets of Predators

To assess canid diets, monthly scat collection was conducted along standardized routes (Pearson 1966) located adjacent to and within each of the seven habitats where prey abundances and canid activities were estimated. Scats were analyzed for bone and hair remains, which were compared to a reference collection, and mammalian prey identified to genus. In particular, two species of *Peromyscus*, *P. leucopus* and *P. maniculatus*, were distinguished together as *Peromyscus* spp. for all analyses associated with canid diets. Avian remains, primarily feathers and bones, were used to identify birds to order, with the exception of pheasant, which was identified to genus. Exoskeletons were used to identify arthropods to Class Insecta or Crustacea. The minimum count of diagnostic parts, primarily teeth, were used to ascertain the number of mammal prey items per scat (Weaver and Hoffman 1979). Coyote and red fox scats were differentiated by

size comparisons following Green and Flinders (1981) and Halfpenny (1986); volume of scat was a differentiating criteria in the event of size overlaps.

In addition, microtine skeletal remains in scat were used to identify juveniles and adults to determine age selection by coyotes. Since microtine teeth continuously erupt, taking cranial measurements is the generally accepted means of aging these individuals (Carleton 1985). However, complete cranial material of prey remains is rarely available in canid scat, due to mechanical breakdown that occurs in the digestive tract (Andrews 1990, personal observation). Patterns of tooth wear, especially variation in enamel patterns of particular molars, have been used to age microtines (Hinton 1926, Martin 1956). Nonetheless, interpretation of microtine age through tooth wear should be interpreted with caution. For this study, microtine prey remains were compared to cranial reference material from individuals of known age. Differentiating criteria for conservative age estimates (juvenile vs. adult) included: size of molars, length of mandibular tooth row (which was shorter in very young individuals), degree of enamal and dentine degradation, and cranial measurements if available.

Activity of Predators

Beginning in March 1994, canid activities were monitored through the use of scent stations. Scent stations were constructed by excavating a 50-cm wide by 10-cm deep depression, rimmed with a 10-cm wide strip of aluminum flashing to inhibit invasive growth from surrounding vegetation, and filled with fine-grained sand. Scent stations

were located along 200-m transects, parallel to the small mammal trapping transects, in each of the seven locations. Transects were spaced ca. 100 m apart, taking into consideration habitat size. Due to range of the predators, there may not have been sufficient separation to avoid visitation by the same individual between lines (Roughton and Sweeny 1982, Diefenbach et al. 1994). However, the scent station transects were not used to make within-habitat activity comparisons, and were effective for obtaining overall activity patterns across Fermilab. Eight scent stations were spaced every 25 m along each transect in six of the locations, for a total of 24 scent stations per location. Three transects with 10 scent stations each were established in Tallgrass Prairie II, where a study on small mammal population dynamics was being conducted (Yunger 1996). As part of the small mammal study, four large vertebrate predator exclosures and four control plots were used to examine effects of predation on small mammal population dynamics (Fig.2). Sixteen additional scent stations were constructed in the winter of 1994-1995, one at each corner of the four predator-access experimental plots. These additional scent stations were monitored in conjunction with a small mammal food supplementation experiment to determine the response of canid foraging activity to within-habitat changes in prey availability. This facilitated a comparison of canid activities at both larger (between-habitat) and smaller (within-habitat) spatial scales. All scent stations were lured by placing a cotton swab dipped in a liquid commercial predator lure (Cronk's Predator 500, Wisscasset, Maine) upright in the middle of the scent station; stations were then run simultaneously for a minimum of two nights, an average of two times per month. Predator

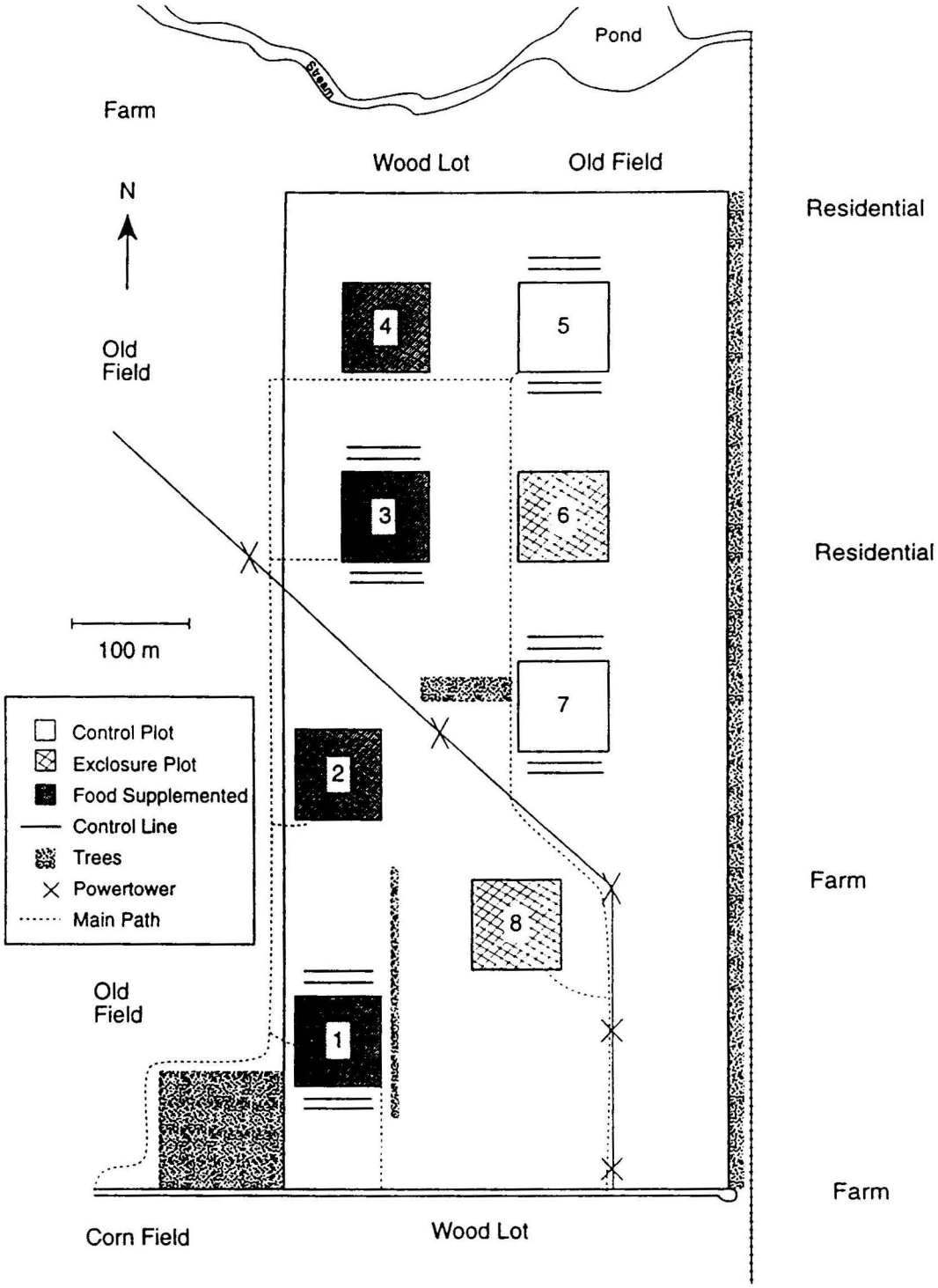

Figure 2. Map of experimental plots at Tallgrass Prairie II, showing predator exclusion and predator access plots, and plots in which the food supplementation experiment was conducted.

activities were ranked from 0 (no activity) to 3 (high activity) based upon the number of tracks left at a scent station. Preliminary trials were conducted to determine the criteria used for this subjective ranking scale.

An index of monthly predator activity was calculated for each predator species (coyote and red fox) in each location by summing corresponding scent station activity levels and dividing by the total number of operative nights [i.e., SSI = ($\sum$A.L. / no. stations) / ($\sum$nights / no. stations) where SSI = scent station index and A.L. = activity level; number of scent stations cancels out of the equation (modified from Linhart and Knowlton 1975)]. Thus, the scent stations quantified between-habitat canid activity across Fermilab as a whole.

Vegetation Analysis

Three different variables were collected on habitat structure for each of the seven locations: 1) vertical foliage density, 2) percent ground cover, and 3) canopy coverage. Vegetation measurements were collected at 24 stations per location, along alternating stations of the small mammal trapping transects. Foliage density was measured using a modified profile board technique (MacArthur and MacArthur 1961). The original technique involved dividing a white board into squares, and moving away from an observer at the same height until half the board was obscured by vegetation. The distance from board to observer was measured to calculate foliage density at a particular height. For this analysis, percent coverage of three 30 x 50-cm profile boards was measured at 0.5

m, 1.0 m and 1.5 m from ground to mid-level of the board. The profile boards were divided into 15, 10 x 10-cm cells. A cell was considered covered if 50% or more of the cell, viewed from a 5 m distance, was obstructed by vegetation. The proportion of cells covered determined percent coverage of an individual board. Readings were taken facing north; based on visual assessment and terrain of all locations, there was no apparent patterning or trending in vegetation structure and diversity between each of the four cardinal directions.

To arrive at a single foliage density value for each study location, the proportion of vegetation coverage was averaged across the three profiles for each of the 24 sampling stations, then the mean of the resulting 24 values was taken. Percent coverages of the three profiles were averaged to represent foliage density at the macrohabitat level, since canids would be presumed to respond to overall vertical structure in their use of a particular habitat rather than responding to subtle microhabitat differences.

Percent ground cover was assessed by the amount of vegetation (herbaceous, woody, and leaf litter) occupying a 1-m^2 quadrat (Brower et al. 1990). Percent ground cover was averaged across all 24 sampling points per location, to arrive at a single value representing a habitat's average amount of ground cover. Canopy coverage was estimated by the presence or absence of vegetation viewed through a vertical ocular tube (James and Shugart 1970). For each particular sampling station, presence of canopy was scored as 1 while absence was scored as 0. The mean of the 24 scored values per habitat represented average canopy coverage.

The vegetation analysis was conducted once in March 1994 and once in August 1994. Vegetation from December through April has characteristically little foliage, typical of winter vegetation, whereas vegetation from June through October is typified by high foliage density, typical of summer. Two months of the year, May and November, represent transitions between seasons and hence, characteristic vegetation. That is, foliage of deciduous trees and shrubs in May is readily apparent but may not have fully "leafed-out" and herbaceous vegetation has yet not achieved its maximum growth. In November, most of the foliage of deciduous trees and shrubs has dropped and the herbaceous vegetation has dried, taking on a characteristically sparse "winter" appearance. Hence, to avoid special classification and vegetation measurements for two of twelve months in the year, it was necessary to include them within one of the two survey periods. For this study, vegetation variables for May were described by the August survey (i.e., high foliage density), and vegetation variables for November were described by the March survey (i.e., low foliage density).

Data Analysis

Availability of Prey

Analysis of small mammal prey abundances from the capture-recapture data was based upon minimum number known alive (MNKA). This estimate was generated for each individual transect per month using Package C. M. R. (Le Boulengé 1987). The estimates were then averaged for the three transects to yield monthly small mammal

species composition and abundance for each habitat. For the analysis of prey available to canids, species abundance estimates were summed over three-month time blocks, corresponding to seasons. The months used to designate each season were Winter: December, January, February; Spring: March, April, May; Summer: June, July, August; Fall: September, October, November. Since canids potentially move and forage over large areas, predator diets were compared to changes in prey availability across Fermilab as a whole. Hence, seasonal prey availability was computed by averaging monthly abundances of all 21 transects, then summing those values corresponding to each season.

Analysis of covariance (ANCOVA), conducted with SAS PROCEDURE GLM (SAS 1990a), was used to compare abundances of the three main prey, identified in the canid diets. Specifically, analyses were conducted to test for significant fluctuations 1) when prey abundances were averaged across the landscape and 2) in prey abundances among each of the seven habitats. ANCOVA can be used to test for an interaction or heterogeneity of slopes (Littell et al. 1991). Temporal change was indicated by crossing the categorical variable (i.e., prey abundances across the landscape or prey abundances per habitat) with the continuous covariate (time). In order to produce a more sensitive analysis, traditional model building techniques were used (Box et al. 1978). That is, non-significant, higher-level interactions were removed from the model to increase the chance of detecting significant lower-level interactions and/or main effects. If no significant sources of variation were detected, the full model was reported. If significant interaction of variables occurred (i.e., heterogeneity of slopes), significance of main effects were

interpreted by carefully inspecting the plotted data. To examine whether canids shifted activity in response to prey, it was necessary to demonstrate both spatial and temporal differences in prey abundances. Hence, canid activities were compared to monthly between-habitat changes in prey availability. For all parametric analyses, inferences were based on type III sum-of-squares and significance accepted at $\alpha = 0.05$.

Diet Selection of Predators

A log-linear analysis was used to examine (1) whether there was a significant difference between prey selection of *C. latrans* and *V. vulpes*, (2) whether canids selected prey in proportion to availability and (3) whether canids switched between alternative prey. Log-linear analysis is used for multidimensional categorical data, in which all variables can be considered dependent variables. The models generated for this analysis are analogous to those in Analysis of Variance (ANOVA; Fienberg 1970, Agresti 1984), except that terms on the dependent variables are discrete or categorical. The approach used in this analysis tests for joint relationships between variables in particular categories and their interactions. Prey consumption, scored according to the total number of occurrences in scats collected for a particular season, was weighted according to prey available. The weighting factor was based on Manly's selectivity measure of type one selection, in which a selected prey individual is replaced in the population by a new individual of the same class (Manly 1974). Weighting takes into consideration resource use (prey consumption) as it pertains to resource availability (prey abundances), rather

than assuming completely random use (Heisey 1985, Edwards 1989). The weighted values represented individual cell frequencies of the underlying contingency table, corresponding to a particular prey class and time period in the log-linear model. Using *SAS PROCEDURE CATMOD (SAS 1990b), a chi-squared goodness of fit statistic was* generated for each term of the log-linear model. Significance was accepted at $\alpha = 0.05$. In addition, a model building approach was used in the analysis. If higher-order interaction terms were not significant, they were removed from the model. If removal of higher-order interaction resulted in notable changes in lower-level interactions or main effects, the reduced model was reported; if removal of an interaction made little difference the full model was reported. A chi-square analysis with continuity correction was performed using SAS PROCEDURE FREQ (SAS 1990b) for the age selection of prey.

Activity of Predators

Multiple regression analysis was used to evaluate the effect prey availability and vegetation structure had on coyote activities. Six independent variables were used in the model: the abundances of the three main prey genera, 1) *Microtus*, 2) *Peromyscus*, and 3) *Sylvilagus*, and the three vegetation variables, 4) vertical foliage density, 5) percent ground cover, and 6) canopy coverage. Each observation in the multiple regression represented a single measure of the independent variable in one of the seven habitats during one of 15 months. Thus, there were 105 observations for each independent variable, or a total of 630 data points for the regression analysis. Outliers were detected

through an influence diagnostic (similar to Cook's D) generated with SAS PROCEDURE REG (1990a). Detected outliers were removed for the subsequent multiple regression analysis if they had a significant influence on the outcome of the model. Similarly, collinearity diagnositics, such as tolerance values and variance inflation factors, indicated a lack of collinearity between the regressors, which justified retention of all independent variables.

Particular within-habitat responses of coyotes to prey abundances were conducted with two separate analyses. First, activities of coyotes around the experimental plots in Tallgrass Prairie II were analyzed using a one-way repeated measures analysis of variance (rmANOVA), with SAS PROCEDURE GLM (SAS 1990a). Inferences were based on Huynh-Feldt adjusted *P*-values for the rmANOVA. Second, a linear regression analysis performed with SAS PROCEDURE REG (SAS 1990a), was used to compare coyote activities against *Peromyscus* abundances in each of the two adjacent habitats, Tallgrass Prairie I and Oakwoods I.

RESULTS

Population Dynamics of Prey

Population dynamics of the small mammals fluctuated dramatically throughout the course of the investigation. The abundance of *Sylvilagus*, across all seven sampling locations, remained relatively constant throughout the duration of the study (Fig. 3). However, the average numbers of *Peromyscus* and *Microtus*, across all seven locations, were at their highest, during this study, in Fall and early Winter 1993 (Fig. 3). Numbers of *Peromyscus* peaked in November 1993, while numbers of *Microtus* peaked earlier, in September of the same year. In late January 1994, a severe ice storm affected the entire study site, which had a profound affect on the numbers of *Peromyscus* and *Microtus*. By February 1994, virtually none of these two species were captured in the live-traps or observed in the field. Voles, especially, were affected, as their numbers remained low throughout the remainder of the study. Although *Peromyscus* never returned to their former high densities, they exhibited a substantially greater recovery than voles, reaching their second highest densities in November 1994, due primarily to the mast response in Oakwoods I. Separate ANCOVA analyses were done for pre- and post- ice storm prey abundance data, due to the extreme non-linearity of the data, and to distinguish between

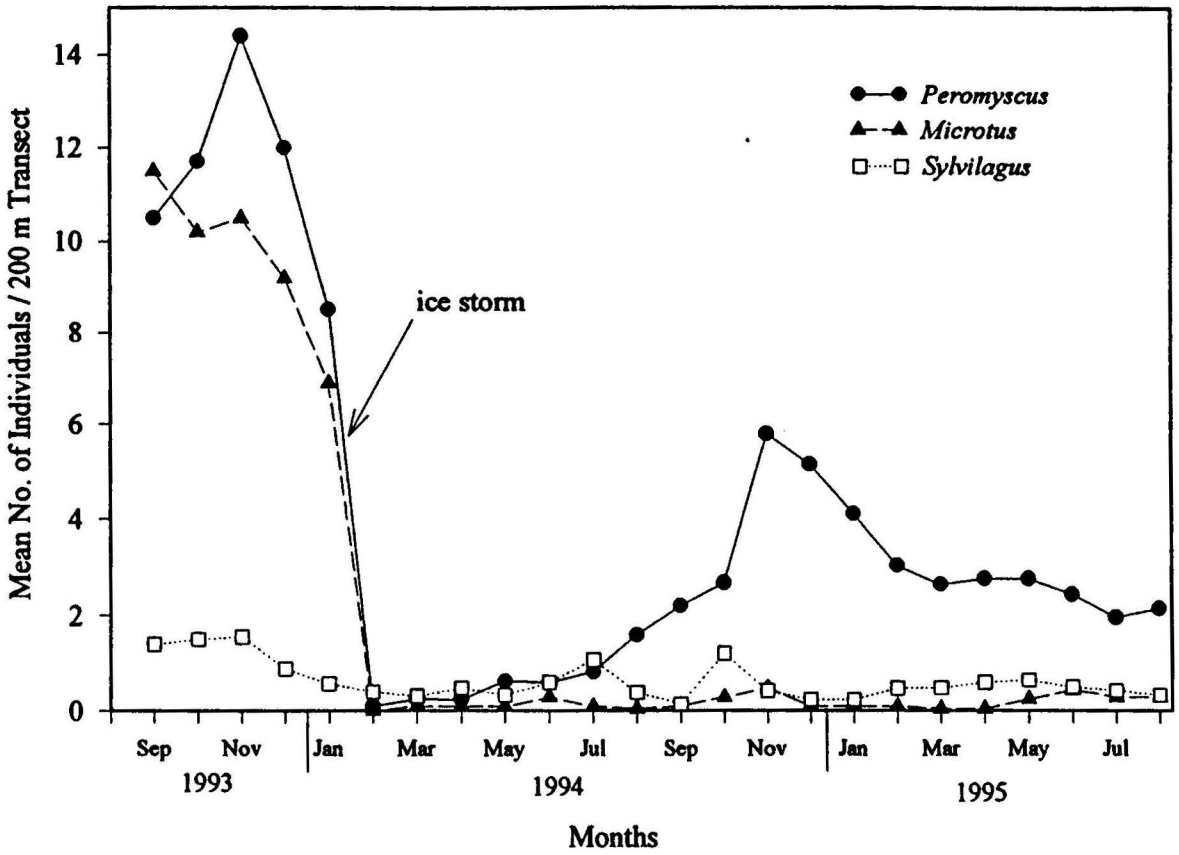

Figure 3. Average abundances of the three main prey of canids over time across all seven sampling locations.

the high density period and low density period for two of the prey (*Microtus* and *Peromyscus*). Results of the pre-ice storm covariate analysis (Table 1), showed a marginally significant time effect and significant species and time^2 sources of variation. The latter two terms indicate that prior to the ice storm, overall numbers of the three species differed significantly from each other, and that the change in numbers over time was explained as a quadratic function (i.e., numbers increased, peaked, then subsequently declined). The significant time effect reflected the decrease in prey numbers immediately following the ice storm.

Table 1

Pre-Ice Storm Covariate Analysis of Minimum Number Known Alive for the Three Main Prey Species Across All Seven Sampling Locations; $R^2 = 0.9686$

Source of Variation	df	MS	*F*	*P*
Time	1	5.768	4.43	0.0684
Species	2	69.348	53.28	0.0001
Time^2	1	9.184	7.06	0.0290
Time^2 x Species	2	1.653	1.27	0.3319
Error	8	1.302		

The post-ice storm covariate analysis (Table 2) showed a significant time effect and a significant time x species interaction. The significant time effect indicated an overall significant increase in the numbers of prey, whereas the significant time x species interaction indicates that the rate of increase of the three species differed over time, primarily attributed to the greater increase in *Peromyscus* as compared to *Microtus* and *Sylvilagus*.

Table 2

Post-Ice Storm Covariate Analysis of Minimum Number Known Alive for the Three Main Prey Species Across All Seven Sampling Locations; $R^2 = 0.7245$

Source of Variation	df	MS	*F*	*P*
Time	1	8.486	14.84	0.0004
Species	2	0.2444	0.43	0.6549
Time x Species	2	7.725	13.51	0.0001
Error	42	1.302		

Predator Dietary Analysis

A total of 388 canid scats were collected between September 1993 and September 1995. Of these, 335 were from coyote and 53 were from red fox. The greatest number of scats were collected between September 1993 and April 1994; after this time, the amount of scats found across all of Fermilab decreased dramatically. The majority were found near the grassland locations; no scats were ever found in Oakwoods II and only a few were found in Oakwoods I. The prey identified in canid scats were divided into ten different categories, and were quantified based upon percent occurrence. These categories were rabbits (*Sylvilagus*), meadow voles (*Microtus pennsylvanicus*), mice (*Peromyscus* spp.), sciurids (Sciuridae), pheasants (*Phasianus*), deer (*Odocoileus*), other vertebrates (e.g., passerines), invertebrates (insects and occasional crayfish), and plant material, which was divided into seeds and herbaceous matter (primarily grass). Three genera, *Microtus*, *Peromyscus*, and *Sylvilagus*, comprised 80.3 % of the 615 individual prey detected in coyote scats and 83.6% of the 61 of the prey identified in red fox scat. The proportions of different prey detected in canid scats were compared to the availability of the prey as determined from the trapping and visual survey data.

Due to the relatively small sample size of red fox scats, data were pooled for the pre- and post-ice storm periods for both canid species (Fig. 4). Prior to the ice storm, *Microtus* comprised the greatest proportion of individual prey detected in both canid diets, followed closely by *Sylvilagus*. However, rabbits represented the greater biomass of prey

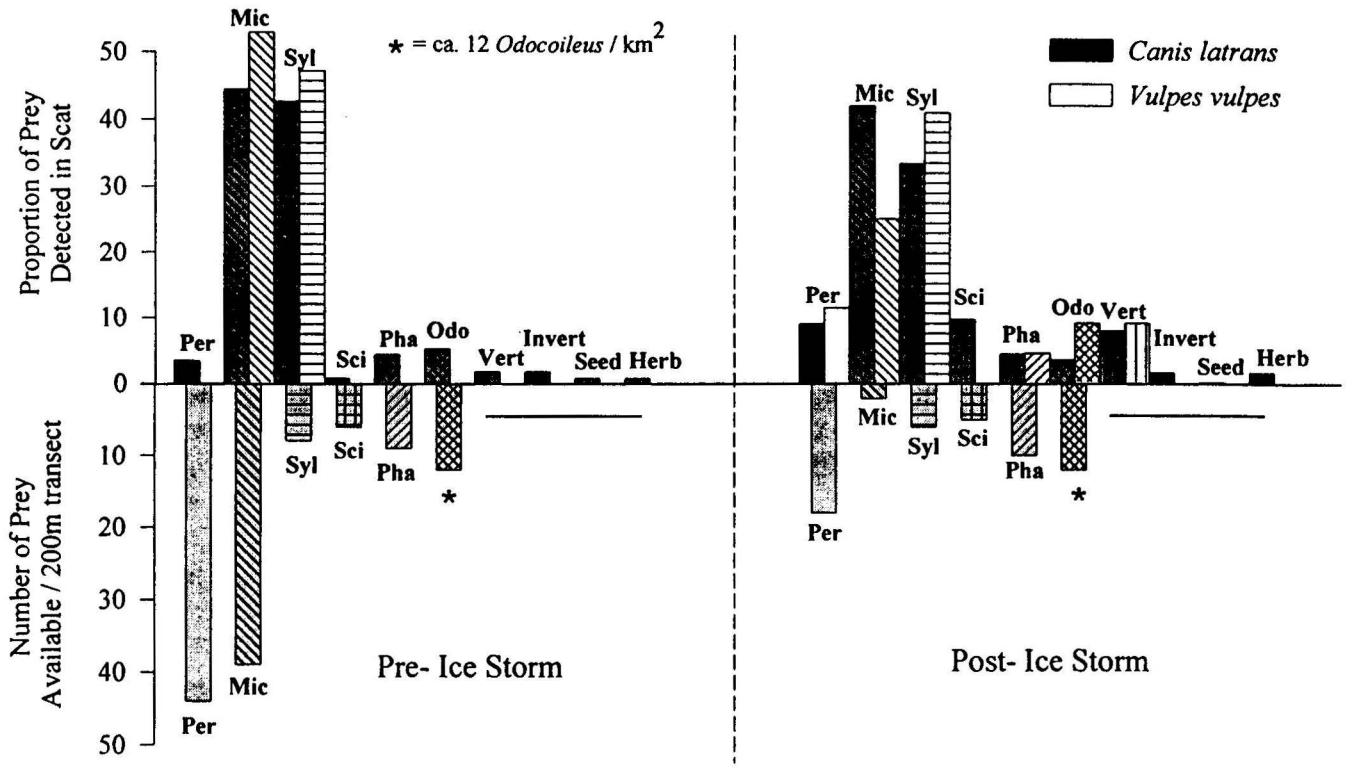

Figure 4. Pre- and post-ice storm comparison of prey consumed by *Canis latrans* and *Vulpes vulpes* vs. prey available. Per = *Peromyscus*; Mic=*Microtus*; Syl=*Sylvilagus*; Sci=Sciuridae; Pha=*Phasianus*; Odo=*Odocoileus*; Vert=Other Vertebrates; Invert=Invertebrates; Seed=Seeds; Herb=Herbaceous material.

consumed. Following the ice storm, *Peromyscus* consumption increased in both canid diets, which was disproportionate to its availability. The availability of *Microtus* decreased dramatically during this time, whereas the number of *Sylvilagus* only decreased slightly. However, the overall trend in coyote diets continued to be the preferential selection of voles, followed by rabbits. Compared to pre-ice storm diets, consumption of pheasant, deer, and other vertebrates increased for red fox from 0% for all three categories to 4.5%, 7.5%, and 9.1%, respectively. This switch, an approximately 30% increase in *Peromyscus* and other prey, compensated for the decrease of *Microtus* in red fox diets. Consumption of sciurids, and other vertebrates increased approximately by 8%, and 6%, respectively, for coyotes following the ice storm.

Using a three-variable saturated model, results of a log-linear analysis comparing the two canids' diets revealed only a significant prey x time interaction (Table 3). When the analysis was re-run with the three-way interaction omitted, there were no significant changes in *P*-values for the interaction terms, but the main effects time and predator became significant. The significant predator effect indicated that overall prey consumption differed between red fox and coyote. However, the significant prey x time interaction showed that both predators switched to alternative prey following the ice storm, albeit proportional to each other. This was attributed to the increased consumption of *Peromyscus* by both predators. Since the log-linear analysis was only conducted with *Microtus*, *Sylvilagus*, and *Peromyscus*, this did not reflect smaller dietary shifts to other prey. The lack of a significant predator x time interaction indicated that even though the

prey consumed by the two predators differed, the relative proportions of prey consumedbetween the two canid species did not change between pre- and post-ice storm.

Table 3

Coyote and Red Fox Diet Selection Prior to and Following the Ice Storm

Source	df	Chi-Square	*P*
Prey	2	1.53	0.4655
Predator	1	32.98	<0.0001
Time	1	33.13	<0.0001
Prey x Predator	2	0.06	0.9728
Prey x Time	2	28.50	<0.0001
Predator x Time	1	0.39	0.5311

The greater number of coyote scats enabled a finer comparison of coyote diets over time, both seasonally and annually (Fig. 5). In Fall and Winter of Year 1, prior to the ice storm, *Microtus* and *Sylvilagus* comprised the greatest proportion of coyote diets, despite the greater number of *Peromyscus* available during that winter. The consumption of *Peromyscus* increased following the ice storm, and exceeded the number of *Microtus* in Summer of Year 1, due to the extremely low availability of voles. Coyotes also fed heavily upon *Sylvilagus* during that same summer. When the availability of voles increased slightly again in Fall of Year 2, *Microtus* consumption once again surpassed the consumption of *Peromyscus* by coyotes. In Winter of Year 2, when *Microtus* numbers declined again, dietary preference shifted to *Sylvilagus*. This was followed by a noticeably higher occurrence of *Microtus* than *Sylvilagus* in coyote scats from the Spring and Summer of Year 2, although vole numbers did not substantially increase that Spring. The apparent trend in coyote diets was the preferential consumption of voles, provided they were at least minimally available, followed by rabbits.

Results of the log-linear analysis of coyote diet selection (Table 4) showed a significant time (corresponding to the eight three-month time blocks) effect, which indicated that coyote prey consumptions changed among the three-month time blocks. Consumptions of the three main prey differed significantly over time as evidenced by the significant prey x time interaction. Thus, coyotes switched between alternative prey over time. Because switching occurred, a post-hoc comparison was made of individual response parameters, corresponding to each prey x time category (Table 5). This was

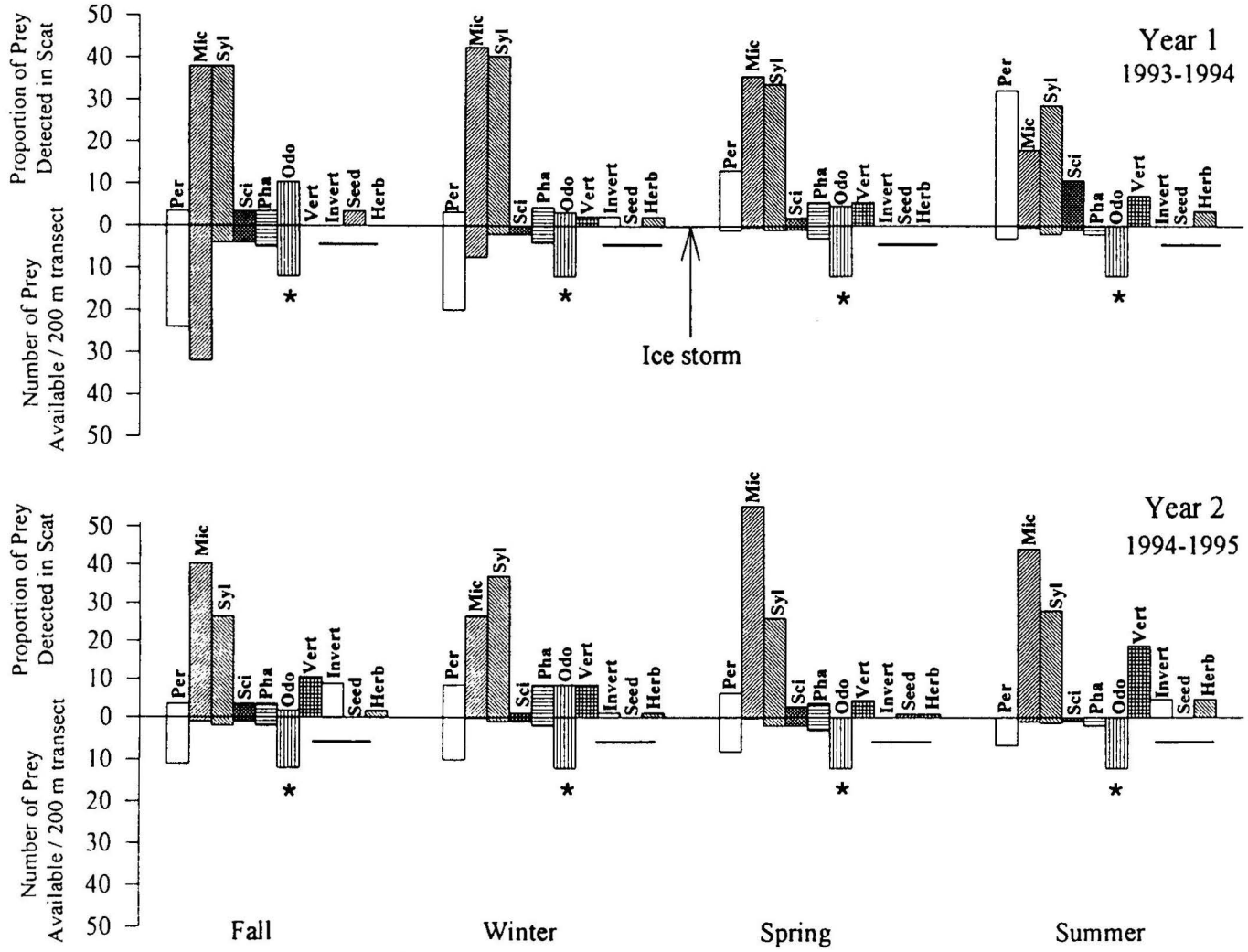

Figure 5. Seasonal comparison of prey consumed by *Canis latrans* vs. prey available. Per=*Peromyscus*; Mic=*Microtus*; Syl=*Sylvilagus*; Sci= Sciuridae; Pha=*Phasianus*; Odo=*Odocoileus*; Vert=Other Vertebrates; Invert=Invertebrates; Seed=Seeds; Herb=Herbaceous material.

Table 4

Coyote Diet Selection of Different Prey Species Over Time

Source	df	Chi-Square	*P*
Prey	2	1.05	0.5914
Time	7	33.13	<0.0001
Prey x Time	14	30.81	0.0059

done by omitting the loglin statement in PROCEDURE CATMOD, which specifies whether the analysis will use a saturated or unsaturated model. Significant *P*-values of the parameters indicated significant dietary shifts, proportional to availability, by coyotes. Based on maximum likelihood estimation, it appeared that coyotes consumed *Microtus* disproportionate to their availability in Winter of Year 1 (Table 5). This is reflected by the high proportion of *Microtus* detected in coyote scats, despite their decreased availability compared to the previous season (Fig. 5). In Spring of Year 1, all three prey consumptions were significant (Table 5). At this time, numbers of these prey had decreased; coyotes were still preferentially feeding on *Microtus*, but consumption of the other two prey increased. This indicated the initiation of a dietary shift by coyotes

Table 5

Maximum Likelihood Parameter Estimates

Time	Prey					
	Microtus		*Peromyscus*		*Sylvilagus*	
	Chi-Square	*P*	Chi-Square	*P*	Chi-Square	*P*
Fall '93	1.86	0.1732	1.15	0.2832	0.71	0.3984
Win '93	9.80	**0.0017**	0.02	0.8203	0.01	0.9130
Spr '94	4.32	**0.0377**	6.11	**0.0134**	26.60	**<0.0001**
Sum '94	1.25	0.2637	1.54	0.2147	0.14	0.7092
Fall '94	0.28	0.5999	0.00	0.9467	0.02	0.8977
Win '94	0.97	0.3236	3.97	**0.0464**	0.55	0.4563
Spr '95	0.02	0.8875	2.17	0.1406	1.51	0.2190
Sum '95	0.01	0.9371	0.33	0.5683	0.02	0.8203

(Fig. 5). The only other significant response category was for *Peromyscus* in Winter of Year 2 (Table 5). At this time, *Peromyscus* were the most abundant of the three main prey, but were not proportionately consumed (Fig. 5). The probabilities of the response parameters did not reflect the switch to *Peromyscus* and *Sylvilagus* that occurred in Year 1. In addition, they did not indicate the disproportionately high consumption of *Microtus* in Fall and Spring of Year 2, nor the lack of *Peromyscus* consumption in Summer of Year 2, despite their relative abundance. This may be due to sensitivity to the weighting factors used for the log-linear analysis, which may mask some of the visually apparent (Fig. 5) shifts in coyote diet.

Coyotes preyed on a significantly greater proportion of juvenile *Microtus* following the ice storm as compared to prior to the ice storm (χ^2=11.655, df = 1, P = 0.001). Of 52 individuals that could be aged, 16.0% and 66.7% were juveniles, pre- and post-ice storm, respectively (Table 6).

Table 6

Age Selection of Voles by Coyotes During Pre- and Post-Ice Storm

		Age	
		Adult	Juvenile
Ice Storm	Pre	21	4
	Post	9	18

Canid Activities

No signs of coyotes were ever found in Oakwoods II, and coyote activities fluctuated rather dramatically between the remaining six locations (Fig. 6). However, the majority of tracks were recorded in the grassland habitats. Tracks of red foxes were found occasionally throughout the study, but their low occurrence precluded analysis of red fox activities.

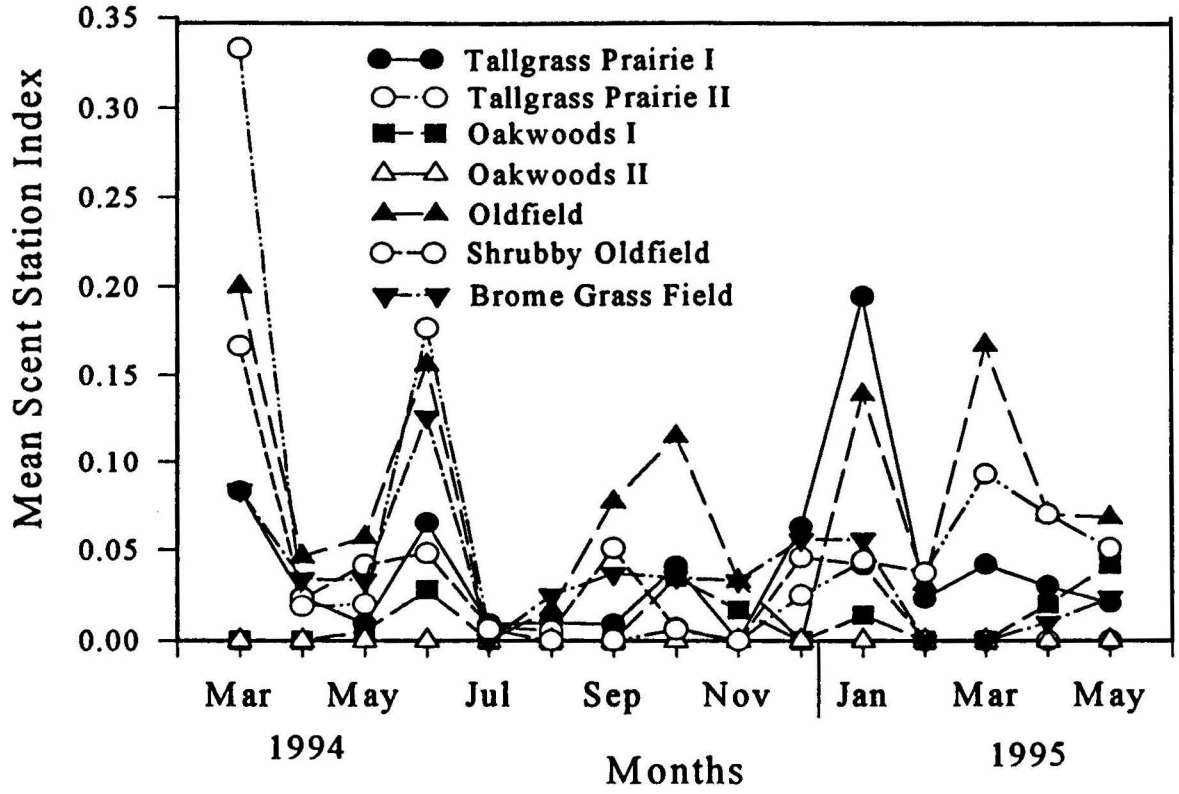

Figure 6. Activities of *Canis latrans* over time between the seven habitats.

Between-Habitat Activities

Variations in prey abundances among each of the seven habitats were plotted for the three main prey species over the time period for which coyote activities were monitored (Fig. 7). The highest *Peromyscus* abundances were documented in November 1994 in Oakwoods I and the highest *Microtus* abundances occurred at the same time in Tallgrass Prairie I. The highest *Sylvilagus* abundances were documented in October 1994 in the Oldfield, with nearly equally high numbers recorded in July 1994 in the two prairie sites, probably following the weaning period of most young rabbits (Hoffmeister 1989). The results of the covariate analysis of these prey abundances among the seven habitats showed significant species, time, and time^2 effects (Table 7). These indicated that the overall numbers of the three species differed significantly from each other, and that the change in numbers over time was explained as a quadratic function. The significant time x species and time^2 x species interactions, indicated that the rate at which species numbers changed differed; this was primarily due to the substantial increase in *Peromyscus* numbers, which is not readily apparent in Figure 7 due to the differences in scale of the three graphs. Furthermore, the significant time x habitat x species and time^2 x habitat x species interactions indicated that the differential rates in changes of numbers of species also changed between the different habitats.

Coyote activities were plotted against each of the three main prey abundances (Fig. 8) and three habitat structure variables (Fig. 9). These graphs represent the partial regression plots of the multiple regression analysis of coyote activity. Each point

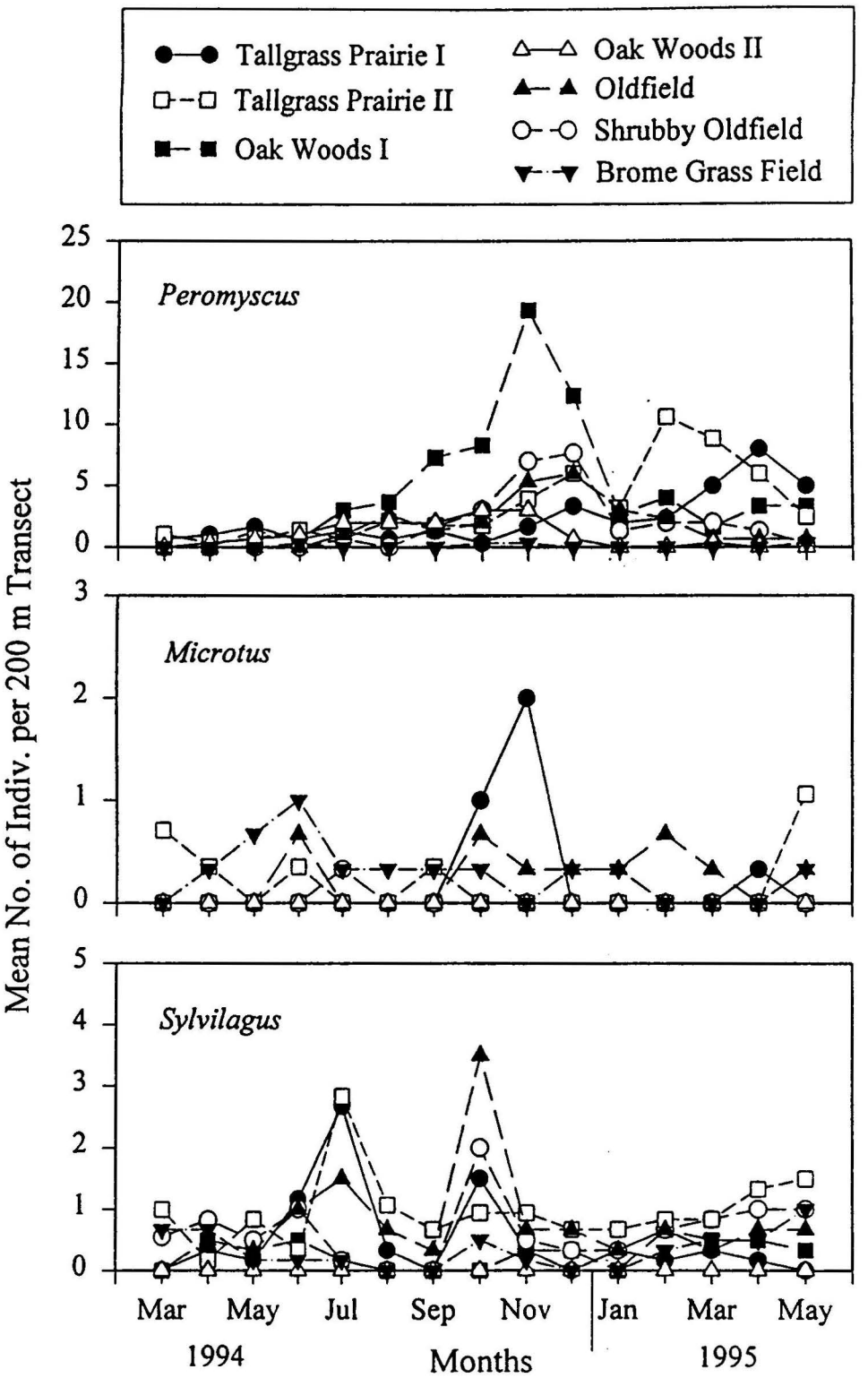

Figure 7. Abundances of the three main prey in each of the seven habitats over time.

Table 7

Results of Covariate Analysis of Minimum Number Known Alive

for the Three Main Prey Among Seven Locations; $R^2 = 0.6581$

Source of Variation	df	MS	*F*	*P*
Time	1	35.774	21.29	0.0001
Habitat	6	2.739	1.63	0.1393
Species	2	10.429	6.21	0.0023
$Time^2$	1	23.186	14.17	0.0002
Time x Habitat	6	6.728	4.00	0.0008
$Time^2$ x Habitat	6	6.784	4.04	0.0007
Time x Species	2	30.743	18.29	0.0001
$Time^2$ x Species	2	19.736	11.74	0.0001
Habitat x Species	12	2.645	1.57	0.0994
Time x Habitat x Species	12	7.584	4.51	0.0001
$Time^2$ x Habitat x Species	12	8.138	4.84	0.0001
Error	264	1.974		

represents a single observation recorded during 1 of 15 months in one of the seven study locations. Separate regression lines indicate negative relationships between coyote activities and each of the independent variables, except for *Microtus* abundance. Results showed that of the variables measured, only *Microtus* abundance and canopy coverage significantly explained coyote activities (Table 8). Also, the relationship between *Microtus* abundance and coyote activity resulted in a significant quadratic response. However, the model explained only 26.5% of the variance. This may be attributed to the large number of zero values recorded for prey abundances. Transformations had a negligible effect on the distribution of the data, and hence were not used for the analysis.

A closer comparison of coyote activity was made between two adjacent habitats with different vegetation structure, Tallgrass Prairie I and Oakwoods I. Results showed that indexed coyote activity, averaged over time, was over three times greater in the prairie (mean = 0.0307, +/-SE = 0.0067) as opposed to the oakwoods (mean = 0.0095, +/-SE = 0.0038) and that these means were significantly different (t = 2.7524, df = 26, P = 0.0106). However, *Peromyscus* abundance (i.e., *P. leucopus*) was two times greater in the oakwoods (mean = 4.7287 individuals, +/-SE = 1.3544) as compared to *Peromyscus* abundance (i.e., *P. maniculatus*) in the prairie (mean = 2.3333 individuals, +/-SE = 0.5539) and that these means were significantly different (t = 1.6369, df = 28, P = 0.1128). Since such discrepancy in activity levels occurred within a particular locality, this provided further evidence that coyote activity was negatively correlated with canopy coverage.

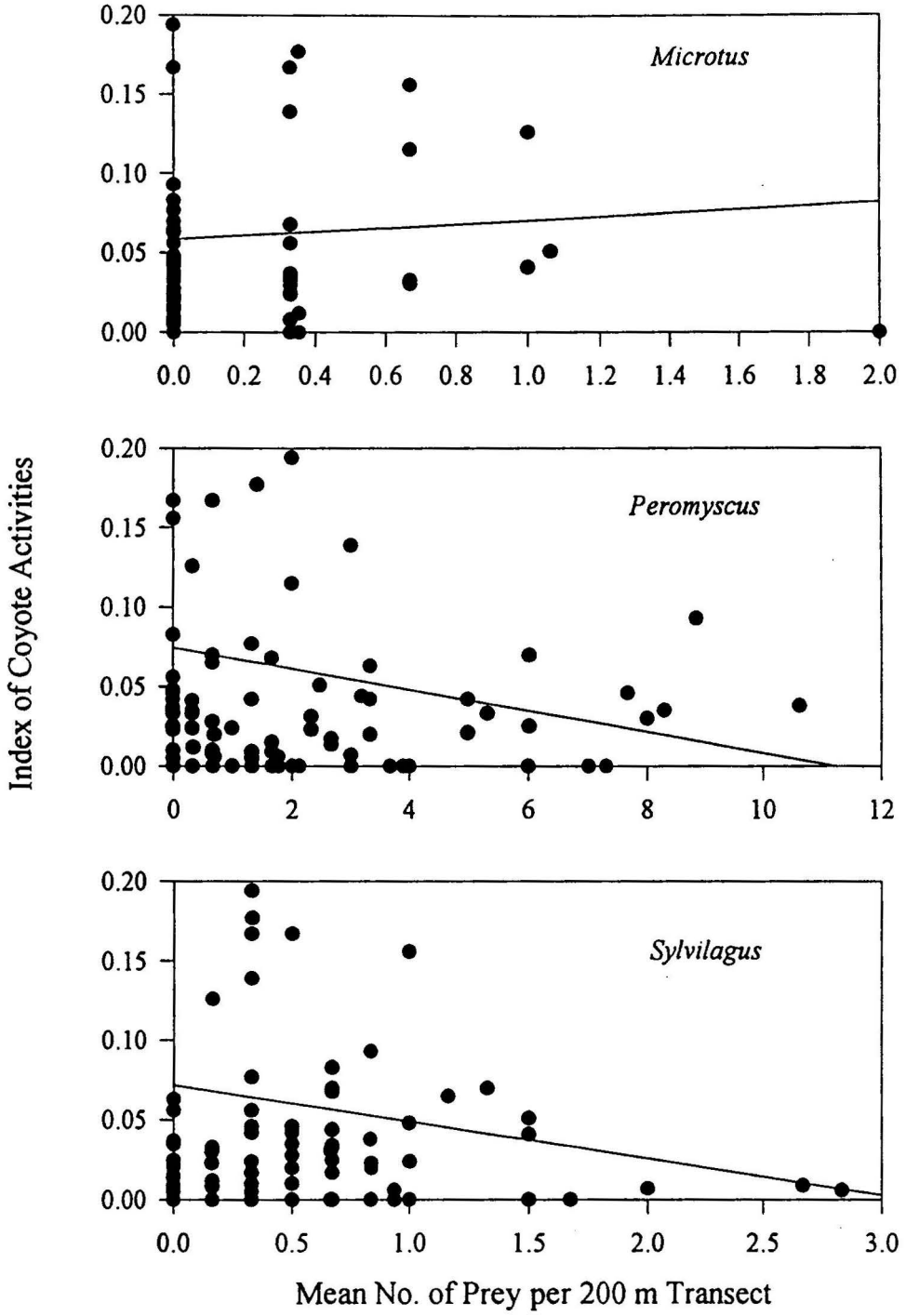

Figure 8. Activities of *Canis latrans* vs. abundances of each of the three main prey.

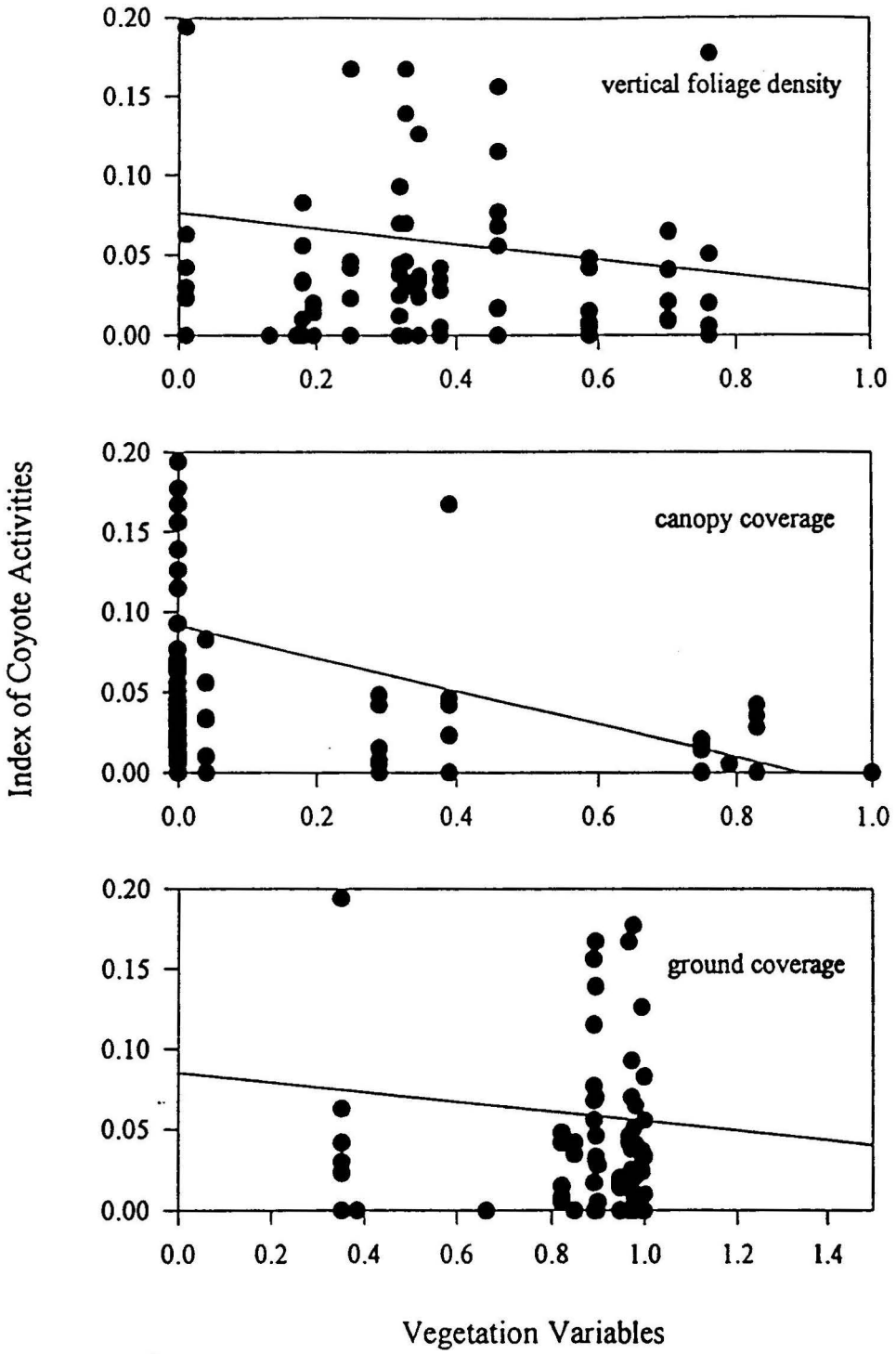

Figure 9. Activities of *Canis latrans* vs. each of the three vegetation variables.

Table 8

Results of Multiple Regression Analysis of Coyote Activity

vs. Abundance of Prey Species and Habitat Variables; $R^2 = 0.2647$

Source	df	MS	*F*	*P*
Model	7	0.0106	0.0106	0.0001
Error	94	0.0022		

Parameter Estimates

Variable	df	b	*P*
Intercept	1	0.0569	0.0231
Peromyscus	1	-0.0001	0.9460
Microtus	1	0.1281	0.0005
Microtus^2	1	-0.0744	0.0025
Sylvilagus	1	0.0048	0.5948
Foliage Density	1	-0.0354	0.2160
Canopy Coverage	1	-0.0392	0.0094
Ground Coverage	1	-0.0126	0.6557

Within-Habitat Activities

The food supplementation experiment in Tallgrass Prairie II was initiated in October 1994. By February 1995, there was a sharp increase (approximately three-fold) in numbers of *Peromyscus* on the food supplemented plots as compared to the unsupplemented plots. Numbers subsequently declined until densities converged on the supplemented vs. unsupplemented plots in May (Yunger 1996). Coyotes responded to the peak in *Peromyscus* densities with mean activities around the food supplemented plots over five times greater than on unsupplemented plots in February 1995 (Fig. 10). Coyote activities around these plots in the ensuing three months reflected the trend in prey (*Peromyscus*) availability. The result was a significant food effect, a marginally significant time effect, and a significant activity x time interaction (Table 9). The interaction reflects the decrease in coyote activity along with the decrease in *Peromyscus* numbers on the food supplemented plots. This demonstrated the ability of coyotes to "cue-in" to abundant patches of food within a particular habitat.

In addition to the food supplementation experiment, the perturbations in Tallgrass Prairie I and Oakwoods I allowed comparisons of activity level changes within these two habitats over time. As previously mentioned, when averaged over time, coyote activity was almost two times greater in the prairie as opposed to the oakwoods. No relationship existed between coyote activity and prey abundance in Tallgrass Prairie I over time (F = 0.003, df = 1, P = 0.9590). It appeared via snow tracking, that coyotes frequently traversed the site and the abundance of *Peromyscus* did not significantly influence coyote

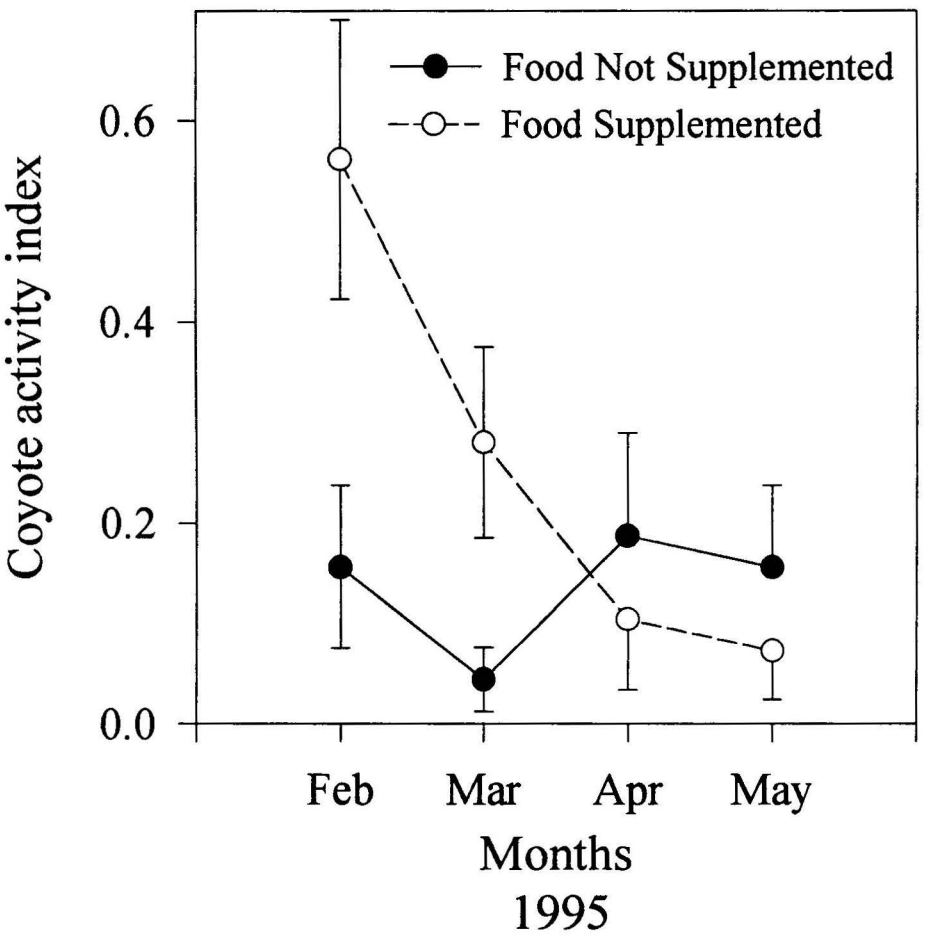

Figure 10. Activities of *Canis latrans* on food-supplemented vs. not supplemented plots.

Table 9

Results of Repeated Measures Analysis of Variance for Coyote Activity

Around Food Supplemented vs. Not Supplemented Plots

Source	df	MS	*F*	*P*
Between Subject:				
Activity	1	0.225	5.60	0.033
Error	14	0.040		
Within Subject:				
Time	3	0.198	2.93	0.055
Activity x Time	3	0.238	3.53	0.031
Error	42	0.067		

activity. That is, the availability of prey in open areas made little difference. However, there was a significant influence of *Peromyscus* abundance on coyote activity in Oakwoods I (Fig. 11). With the inclusion of a one-month time lag, coyote activity was significantly correlated with *Peromyscus* abundance ($F = 12.738$, df = 1, $P = 0.0044$), and addition of a quadratic term (*Peromyscus* abundance squared), explained an additional ten percent of the variance in coyote activity (Table 10). Without the inclusion of a time lag, activity in this habitat was not correlated with *Peromyscus* abundance ($F = 0.523$, df = 1, $P = 0.4835$), nor were the inclusion of further time lags (two-month time lag: $F = 0.323$, df = 1, $P = 0.5822$; three-month time lag: $F = 0.760$, df = 1, $P = 0.4059$).

Table 10

Results of Regression Analysis of *Canis latrans* Activity With a One-Month Time Lag vs. Abundance of *Peromyscus* squared ; $R^2 = 0.6245$

Source of Variation	df	MS	*F*	*P*
Model	1	0.00093	18.294	0.0013
Error	11	0.00005		

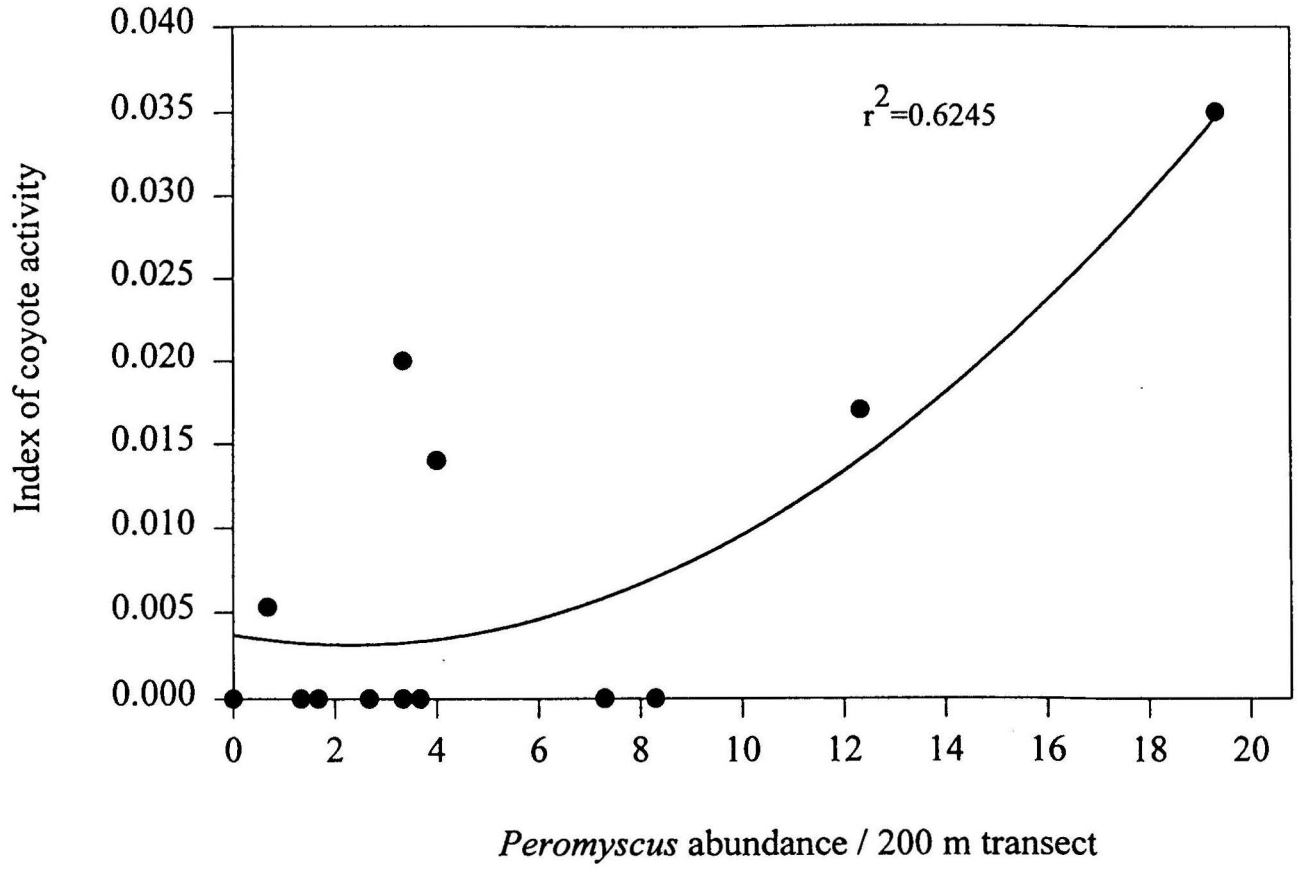

Figure 11. Activities of *Canis latrans* with a one-month time lag, in Oakwoods I vs. abundance of *Peromyscus*.

DISCUSSION

Canid Diets

Both the coyote and red fox are considered to be generalist predators. That is, they tend to feed upon a wide range of food items, which may be linked to temporal and spatial resource availability. In addition, red fox have been considered to be more omnivorous, overall, than coyotes, but this may be questionable, based on some of the reported literature and results of this study. However, in this investigation, both these species behaved similar to small mammal specialists, since the majority of their diets were consistently comprised of three small mammal prey: *Microtus*, *Sylvilagus*, and *Peromyscus*. Due to a small sample size of red fox scats, comparisons of coyote and red fox diets were made between two time periods: prior to a severe ice storm, when small mammal densities were relatively high, and after the ice storm, when small mammal densities were relatively low. This perturbation provided the opportunity to test for 1) predator switching to alternative prey, given the drastic change in prey numbers, and 2) change in diet composition between these two sympatric canids. Prior to the ice storm, *Microtus* comprised the greatest proportion of both coyote and red fox diets, followed by *Sylvilagus*. Although, the rabbits accounted for the greatest biomass of prey consumed. Hence, when small mammal densities were relatively high, there was not much difference

in coyote and red fox consumptions. This may be explained by the fact that when prey is plentiful, the predators could tolerate greater niche overlaps.

Yet, as indicated by the significant predator effect in the log-linear analysis, the two canids' diets differed significantly from one another over time. The overall differences were attributed primarily to their post-ice storm diets. Both canids showed a similar switch to *Peromyscus* after the ice storm. However, coyotes continued to preferentially select *Microtus*, overall. Red fox, alternatively, consumed more *Sylvilagus* than any other prey; hence, rabbits represented the most preferred prey, both in number consumed and biomass. Shifts to other prey were also slightly different, but were not indicated by the log-linear analysis, in which only the three main prey were used for diet comparisons. This may be why there was not a significant predator x prey x time interaction, which would have indicated different dietary switches by the canids, between the two time periods.

Previous studies have shown that coyotes exclude sympatric red fox from areas within their home ranges. Thus, these canids may coexist through spatial partitioning of resources. In this study, the overall differences in prey consumption of these predators were important in explaining a second potential mechanism for coexistence, through resource partitioning. This would be particularly important when small mammal numbers declined, as fewer overlaps in niche requirements would be expected. Therefore, dietary differences could provide a mechanism for coexistence. Nonetheless, very few scats or tracks of red fox were found in the post-ice storm period as compared to before. Although the movements of individual canids were not known, it has been shown that

canids may expand their home ranges as prey availability decreases, in an effort to find prey. If coyotes in this study responded similarly, there may not have been enough prey immediately following the ice storm to partition resources, and hence, red fox would be *displaced through interference competition with the more aggressive, competitively* dominant coyote.

There was a sufficient sample size of coyote scats to enable a finer (i.e., seasonal) comparison of diet in relation to prey availability. Hence, the seasonal dietary analysis revealed details of prey switching that were masked when coyote diets were pooled for the entire pre- and post- ice storm time periods. As previously mentioned, coyotes, preferentially consumed voles, followed secondly by rabbits, and thirdly, mice, overall. In Summer 1994, approximately four months after the ice storm, coyotes switched to mice and rabbits after vole numbers remained extremely low. By Fall 1994, *Microtus* numbers increased slightly, and coyotes responded simultaneously by once again preferentially selecting voles. A similarly rapid response occurred in the subsequent season, Winter 1994-1995. Vole numbers again declined, and coyotes switched to *Sylvilagus*. Thus, outside of the seasons in which coyotes switched to mice or rabbits, voles were the preferred prey, despite their low availability, both in absolute numbers, and relative to other prey species. Most notably, voles were the most highly consumed prey of coyotes in both Spring 1994 and Spring 1995, when virtually no *Microtus* were captured during the live-trapping surveys. In conjunction with the canid dietary work, Cooper (unpublished

data), found that Great-horned Owls, *Bubo virginianus*, also preferentially consumed voles, overall.

One explanation for how predators continued to consume voles in such disproportionately high numbers, when monthly trap surveys indicated that numbers were extremely low, was revealed through age selection of this prey. Using molar size, conservative measures of dentine and enamel degradation, and cranial measurements when available, microtine remains were classified as from either very young individuals or adults. A chi-square analysis indicated that prior to the ice storm, coyotes consumed a greater proportion of older voles, but then consumed a greater proportion of very young voles after the ice storm. Based on cranial remains, Cooper (unpublished data) also found that Great-horned Owls consumed a greater proportion of very young voles after the ice storm as compared to before. Following the ice storm, which occurred during the voles non-reproductive period, fewer adult voles remained. Once reproduction started up again, the post-ice storm vole populations could potentially be comprised of a greater proportion of young voles than the pre-ice storm populations. Based on the low capture rates of voles and age of remains found in scats and pellets, predators were apparently consuming juvenile *Microtus* before they had a chance to enter the trappable population (i.e., become territorial individuals or dispersers). Additionally, by finding and consuming young *Microtus* 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

corroborated by data from Yunger's (1996) concurrent investigation of small mammal population dynamics at Tallgrass Prairie II, which showed that vole numbers were significantly greater on predator-excluded plots versus predator-access plots.

Canid Activities

Relationship to Diet

Coyotes exhibit flexible spatial activity patterns that can be seen by regional variations in home range size. For example, coyotes inhabiting the open plains of the central and western U. S. have home ranges encompassing approximately 20 to 60 km^2 (Andelt et al. 1979, Sargeant et al. 1987), whereas their midwestern counterparts may have home ranges of only 13 km^2 (Cypher 1991). This variation is often correlated with resource availability (Calhoun 1955). Furthermore, coyote home range sizes may increase when the availability of prey decreases. Such changes in activity may occur seasonally, in response to variations in food availability (Andelt et al. 1987).

In this study, coyote activities were partially explained by the abundance of their most preferred prey, *Microtus pennsylvanicus*. This was reflected as a significant effect in the multiple regression analysis of coyote activity. Even though the overall model was significant, this did not explain a major proportion of the variance in coyote activities. This may be attributed to the high number of zero values, due to the extremely low numbers of voles during most of the study. Despite such low availability, it is interesting that coyotes still responded positively to voles, by the relatively high proportion of voles

consumed and greater activity in areas that they inhabited. Surprisingly, overall activities were not correlated with abundance of the second most preferred prey, *Sylvilagus floridanus*. This could possibly be attributed to the fact that cottontail rabbits are often found along habitat edges. Although some of the scent station transects were located within habitat areas where rabbits were found, coyotes could have spent more time foraging for rabbits along these edges where transects were not located.

In addition to large-scale (among habitat) responses to prey availability, coyotes also responded to smaller-scale (within-habitat) prey availability. This was demonstrated in Tallgrass Prairie II, as coyote activities were correlated with experimentally manipulated abundant patches of prey. Specifically, the high level of activity and subsequent decrease in coyote activities detected on scent stations around the predator-access, food manipulated plots paralleled the change in *Peromyscus* densities. Hence, once *Peromyscus* decreased following a peak in densities on these plots, coyote activity likewise diminished. A consequence of predators feeding within these abundant patches was a rapid turnover of prey (Yunger 1996). Since *Microtus* were never highly abundant during the time in which scent station monitoring was conducted, a similar test of within-habitat coyote activity response to abundant patches of this prey was not feasible. However, coyotes could quite possibly have been "cueing-in" to localized patches of *Microtus*, given that they were still the principal part of coyote diets despite their low availability. Although the scent station transects were effective in discerning overall trends

(i.e., between-habitat comparisons) in coyote activity, they were not intended to indicate finer-scale responses that would reflect these localized responses within the landscape.

Habitat Use

Coyote activity fluctuated greatly over time; thus, there were no clear temporal patterns in activity among habitats. However, overall spatial patterns indicated a preferential use of grasslands, and avoidance of woodlands. Throughout the duration of the study, there was no evidence of coyote tracks or scat in Oakwoods II, a mature woodlot with few gaps in its overstory. Although its entire western edge bordered a tallgrass prairie, there was a clear boundary between prairie and woodlot. Also, Oakwoods I experienced relatively little coyote activity during most of the study. When coyote tracks were found, they were generally along the grassy areas at its margins. The shrubby oldfield, characterized by a heterogeneous mix of dense shrubs, shrub-grassland mixture, and areas of small aspen stands, experienced slightly more activity, overall, then the woodlots, but tracks were again found primarily along more open grassy areas, paths, and the western edge of this habitat which bordered a tallgrass prairie. These observations were supported by the significant negative relationship of canopy coverage to coyote activity in the multiple regression analysis. However, voles, the most common prey in coyote diets, were not found in the woodlots. Rabbits, the second most preferred prey, were occasionally found in Oakwoods II but not in Oakwoods I. Yet, if habitat use patterns had been strictly correlated with prey availability, 1) significant effects of habitat

vegetation variables would not have been detected, or 2) collinearity of prey abundances with vegetation variables would have been observed.

Based on home range studies of coyotes in southern Illinois (Priest 1986, Cypher 1991), the number of adult coyotes at Fermilab could have ranged from two to eight individuals (one to three pairs plus possible associated yearlings). If only a couple of individual coyotes were present at Fermilab, habitat selectivity of grasslands could reflect individual (or pair) preferences. Alternatively, the selective utilization of grasslands, may be related, in part, to the historical range of coyotes. Prior to European settlement, coyotes occupied the Southwest and central Plains regions of the U. S., from the Rocky Mountains east to the Mississippi River, and from southern Alberta, Canada south to central Mexico. Clearing of forests and extermination of the wolf facilitated the north and eastward expansion of coyotes. Coyotes moved northward along the Great Lakes, and colonized the northeastern U. S. by the 1940s (Richens and Hugie 1974). By about the same time, coyotes had also colonized the Midwest (Moore and Parker 1983). Most coyotes inhabit deserts and grasslands, although some coyotes can be currently found in spruce forest habitats of Alberta down into pine-hardwood forests of the Southeast. In the southeastern United States, it was found that coyotes in forested regions tend to utilize open, non-forested areas in a greater proportion than that available (Holzman et al. 1992). In northern forested areas during the winter, coyotes will tend to travel and forage in areas where snow is shallower or more densely packed, which is generally correlated with more open areas (Todd et al. 1981, Murray et al. 1994). Hence, open habitats may not

only serve as sites in which prey is easier to find and procure, but as areas facilitating dispersal (e.g., between habitats). Snow tracking at Fermilab indicated that grasslands were also used as "dispersal corridors." Habitats such as the brome grass field and tallgrass prairie were sometimes bisected by coyote tracks following a straight path of travel. The preferential use of grasslands may explain why chipmunks and tree squirrels, which were moderately common in the woodlands, were rarely detected in coyote diets.

It was previously demonstrated how coyotes respond spatially to abundant patches of prey. The Fall 1994 perturbations in Tallgrass Prairie I (fire) and Oakwoods I (high mast) allowed testing of a temporal response of coyote activity to increased abundance of prey. Despite the fact that the multiple regression analysis showed coyote activity to be negatively related to wooded areas (i.e., they did not forage in nor tend to traverse woodlots), a "super-abundant" source of prey could provide an exception to this norm. Specifically, during fall 1994, *Peromyscus* densities in Oakwoods I were two times greater than prey abundances at any other location. Local abundances of prey in the prairie, an area preferentially utilized by coyotes, could also have attracted coyotes to the adjacent woodlot. When coyote activities for these habitats were compared, it was found that there was no discernible response in Tallgrass Prairie I. However, coyote activity increased significantly in Oakwoods I, with an approximate one-month time lag from the peak in *Peromyscus* numbers. Thus, coyote activity in this habitat increased substantially in December, following the November peak in *Peromyscus* numbers. This is somewhat similar to the closely tracked spatial response to *Peromyscus* numbers due to the food

supplementation experiment in Tallgrass Prairie II. Perhaps coyotes, which did not frequently utilize Oakwoods I, took longer to "cue-in" to the rich supply of prey. However, coyotes did respond within a time period in which *Peromyscus* were still moderately abundant in the woodlot as evidenced by lack of significant correlation with a two- or three-month lag in activities. This indicates why the quadratic response of coyote activity to *Peromyscus* abundances in the woodlot helped to further explain the observed variation in coyote activity. That is, during low *Peromyscus* abundance, coyotes did not effectively utilize that habitat. Similarly, coyote activity in the oakwoods was not related to very high *Peromyscus* abundance, but was correlated with moderate prey numbers, as was reflected by the one-month response lag.

The lack of response in Tallgrass Prairie I can be attributed to dispersal as well as foraging activities. Since coyotes frequently traversed this habitat, significant changes in foraging activities could be masked by excessive "noise" due to dispersal movements. The presence of both types of habitat utilization patterns was corroborated by winter snow tracking. When coyotes foraged, their paths meandered or appeared more erratic as prey were being tracked. Clumps of vegetation were investigated for hidden prey. This is contrasted to dispersal movements, which appear much more purposeful and tend to follow a straight line of travel.

General Conclusions

Canids exhibit flexible behavioral patterns that can be reflected through their diets and activities. Both coyotes and red fox showed the ability to switch to alternative prey, given a dramatic change in prey availability. However, they tended to forage on and switch between a select number of prey. This combination of switching and prey selectivity may reflect the most efficient means of foraging for these predators. That is, they may be striking a balance between choosing prey which are smaller and relatively easier to handle and feeding on prey for which they have developed a specific search image. Responding within a relatively short time period to abundant patches of prey, as was demonstrated with coyotes, further facilitates a more efficient means of foraging. However, the preferential utilization of open areas, which facilitate movements and the general procurement of prey, could represent a constraint during periods of very low prey densities.

Furthermore, the dynamics of predator-prey interactions were elucidated by monitoring prey changes within particular habitats and the related responses of predators both within habitats and across the landscape. Hence, the variety of spatial scales utilized by vertebrate predators should be accounted for in future investigations of their foraging behavior.

LITERATURE CITED

Akçakaya, H. R. 1992. Population cycles of mammals: evidence for a ratio-dependent predation hypothesis. Ecological Monographs 62:119-142.

Agresti, A. 1984. Analysis of ordinal categorical data. John Wiley and Sons, New York, New York, USA.

Akre, B. G., and D. M. Johnson. 1979. Switching and sigmoid functional response curves by damselfly naiads with alternative prey available. Journal of Animal Ecology 48:703-720.

Andelt, W. F., and P. S. Gipson. 1979. Home range, activity, and daily movements of coyotes. Journal of Wildlife Management 43:944-955.

Andelt, W. F., J. G. Kie, F. F. Knowlton, K. Cardwell. 1987. Variation in coyote diets associated with season and successional changes in vegetation. Journal of Wildlife Management 51:273-277.

Andrews, P. 1990. Owls, caves, and fossils. The University of Chicago Press, Chicago, Illinois, USA.

Anthony, R. G., L. J. Niles, an J. D. Spring. 1981. Small-mammal associations in forested and old-field habitats--a quantitative comparison. Ecology 62:955-963.

Arnold, D. A. 1956. Red foxes of Michigan. Michigan Department of Conservation. 48 pp.

Baker. R. H. 1983. Michigan mammals. Michigan State University Press, Detroit, Michigan, USA.

Beddington, J. R., M. P. Hassell, and J. H. Lawton. 1976. The components of arthropod predation. II. The predator rate of increase. Journal of Animal Ecology 45:165-185.

Bekoff, M., T. J. Daniels, and J. L. Gittleman. 1984. Life history patterns and the comparative social ecology of carnivores. Annual Review of Ecology and Systematics 15:191-232.

Best, L. B., K. E. Freemark, J. J. Dinsmore, and M. Camp. 1995. A review and synthesis of habitat use by breeding birds in agricultural landscapes of Iowa. American Midland Naturalist 134:1-29.

Box, G. E. P., W. G. Hunter, J. S. Hunter. 1978. Statistics for experimenters, and introduction, to design, data analysis, and model building. John Wiley and Sons, New York, New York.

Breitenmoser, U., and H. Haller. 1993. Patterns of predation by reintroduced European lynx in the Swiss Alps. Journal of Wildlife Management 57:135-144.

Brillhart, D. E., and D. W. Kaufman. 1995. Spatial and seasonal variation in prey use by coyotes in north-central Kansas. Southwestern Naturalist 40:160-166.

Brower, J., J. Zar, and C. von Ende. 1990. Field and laboratory methods for general ecology. Wm. C. Brown Publishers, Dubuque, Iowa, USA.

Brown, J. H. 1995. Macroecology. The University of Chicago Press, Chicago, Illinois, USA.

Byre, V. J. 1989. The Birds of Fermi National Accelerator Laboratory: their seasonal occurrence and breeding activity, including an annotated list of species. Bulletin of the Chicago Academy of Sciences. Vol. 14, No. 4. 37 pp.

Cabot, W. B. 1920. Labrador. Small, Maynard, and Company, Boston, Massachusetts, USA.

Calhoun, J. B. 1955. A technique for investigating the distance parameter of home range. Journal of Mammalogy 36:45-52.

Carleton, M. D. 1985. Macroanatomy. Pages 116-175 *in* R. H. Tamarin, editor. Biology of the New World *Microtus*. Special Publication No. 8. The American Society of Mammalogists, USA.

Catling, P. C., and R. J. Burt. 1995. Why are red foxes absent from some eucalyptus forests in eastern New Wales? Wildlife Research 22:535-546.

Cavallini, P., and S. Lovari. 1994. Home range, habitat selection and activity of the red fox in a Mediterranean coastal ecotone. Acta Theriologica 39:279-287.

Clark, F. W. 1972. Influence of jackrabbit density on coyote population change. Journal of Wildlife Management 36:343-356.

Clark, J. D., J. E. Dunn, K. G. Smith. 1993. A multivariate model of female black bear habitat use for a geographic information system. Journal of Wildlife Management 57:519-526.

Clarke, B. 1962. Balanced polymorphism and the diversity of sympatric species. Pages 47-50 *in* D. Nichols, editor. Taxonomy and Geography. Systematics Association Publication No. 4. Academic Press, London UK.

Connell, J. H. 1978. Diversity in tropical rainforests and coral reefs. Science 199:1302-1310.

Cook, D. B., and W. J. Hamilton, Jr. 1944. The ecological relationships of red fox food in eastern New York. Ecology 25:91-104.

Cook, S. F. 1959. The effects of fire on a population of small rodents. Ecology 40:102-108.

Cornell, H. 1976. Search strategies and the adaptive significance of switching in some general predators. American Naturalist 110:317-320.

Cypher, B. L. 1991. Coyote foraging dynamics, space use, and activity relative to resource variation at Crab Orchard National Wildlife Refuge, Illinois. Ph.D. Dissertation. Southern Illinois University.

Cypher, B. L., A. Woolf, and D. C. Yancy. 1993. Transactions of the Illinois Academy of Science 86:145-152.

Dale, B. W., L. G. Adams, and R. T. Bowyer. 1994. Functional response of wolves preying on barren-ground caribou in a multiple-prey ecosystem. Journal of Animal Ecology 63:644-652.

Dearborn, N. 1932. Foods of some predatory fur-bearing mammals of Michigan. University of Michigan School of Forestry and Conservation, Bulletin No. 1:20-25.

DeJong, J. 1995. Habitat use and species richness of bats in a patchy landscape. Acta Theriologica 40:237-248.

Dekker, D. 1989. Population fluctuations and spatial relationships among wolves, *Canis lupus*, coyotes, *Canis latrans*, and red foxes, *Vulpes vulpes*, in Jasper National Park, Alberta. Canadian Field-Naturalist 103:261-264.

Diamond, J. 1986. Overview: laboratory experiments, field experiments, and natural experiments. Pages 3-22 *in* J. Diamond and T. J. Case, editors. Community Ecology. Harper and Row, New York, New York, USA.

Dice, L. R. 1925. A survey of the mammals of Charlevoix County, Michigan, and vicinity. University of Michigan, Museum of Zoology, Occasional Papers No. 159, 33 pp.

Diefenbach, D. R., M. J. Conroy, R. J. Warren, W. E. James, L. A. Baker, and T. Hon. 1994. A test of the scent-station survey technique for bobcats. Journal of Wildlife Management 58:10-17.

Dunk, J. R., and R. J. Cooper. 1994. Territory-size regulation in Black-shouldered Kites. The Auk 111:588-595.

Edwards, T. C. 1989. The ontogeny of diet selection in fledgling ospreys. Ecology 70:881-896.

Egoscue, H. J. 1975. Population dynamics of the kit fox in western Utah. Bulletin of Southern California Academy of Sciences 74:122-127.

Elton, C. S. 1942. Voles, mice, and lemmings: problems in population dynamics. Clarendon Press, Oxford, UK.

Erlinge, S., G. Goransson, L. Gansson, G. Hogstedt, O. Liberg, I. N. Nilsson, T. Nilsson, T. von Schantz, and M. Sylven. 1983. Predation as a regulation factor in small rodent populations in southern Sweden. Oikos 40:36-52.

Erlinge, S. 1987. Predation and noncyclicity in a microtine population in southern Sweden. Oikos 50:347-352.

Errington, P. L. 1935. Food habits of midwest foxes. Journal of Mammalogy 16:192-200.

Fienberg, S. E. 1970. The analysis of multidimensional contingency tables. Ecology 51:419-433.

Finerty, J. P. 1980. The population ecology of cycles in small mammals. Yale University Press, New Haven, Connecticut, USA.

Fryxell, J. M. and C. M. Doucet. 1993. Diet choice and the functional response of beavers. Ecology 74:1297-1306.

Geffen, E., and D. W. Macdonald. 1993. Activity and movement patterns of Blanford's foxes. Journal of Mammalogy 74:455-463.

Getz, L. L. 1989. A 14-year study of *Blarina brevicauda* populations in east-central Illinois. Journal of Mammalogy 70:58-66.

Getz, L. L., L. Verner, F. R. Cole, J. E. Hoffman, and D. E. Avalos. 1979. Comparisons of population demography of *Microtus ochrogaster* and *Microtus pennsylvanicus*. Acta Theriologica 24:319-349.

Getz, L. L., J. E. Hoffman, B. J. Klatt, L. Verner, F. R. Cole, and R. L. Lindroth. 1987. Fourteen years of population fluctuations of *Microtus ochrogaster* and *M. pennsylvanicus* in east central Illinois. Canadian Journal of Zoology 64:1317-1325.

Green, J. S., and J. T. Flinders. 1981. Diameter and pH comparisons of coyote and red fox scats. Journal of Wildlife Management 45:765-767.

Griffiths, K. J. 1969. The importance of coincidence in the functional and numerical responses of two parasites of the European pine sawfly *Neodiprion sertifer*. Canadian Entomologist 101:673-713.

Gustafson, E. J., G. R. Parker, and S. E. Backs. 1994. Evaluating spatial pattern of wildlife habitat--a case study of the Wild Turkey (*Meleagris gallopavo*). American Midland Naturalist 131:24-33.

Halfpenny, J. 1986. A field guide to mammal tracking in North America. Johnson Publishing Company, Boulder, Colorado, USA.

Hall, E. R. 1981. The mammals of North America. John Wiley & Sons, Inc., New York, New York, USA.

Hamlin, K. L., S. J. Riley, D. Pyrah, A. R. Dood, ad R. J. Mackie. 1984. Relationships among mule deer fawn mortality, coyotes, and alternate prey during summer. Journal of Wildlife Management 48:489-499.

Hanski, I. 1991. The functional response of predators: worries about scale. Trends in Ecology and Evolution 6:141-142.

Harris, L. D. and G. B. Bowman. 1980. Vertebrate predator subsystem. Pages 591-607 *in* Breymeyer and Van Dyne, editors. Grasslands, systems analysis and man. Cambridge University Press, Cambridge, UK.

Harrison, D. J., J. A. Bissonetle, and J. A. Sherburne. 1989. Spatial relationships between coyotes and red foxes in eastern Maine. The Journal of Wildlife Management 53:181-185.

Hassell, M. P. 1971. Mutual interference between searching insect parasites. Journal of Animal Ecology 40:473-486.

-----. 1978. The dynamics of arthropod predator-prey systems. Princeton University Press, Princeton, New Jersey, USA.

Heisey, D. M. 1985. Analyzing selection experiments with log-linear models. Ecology 66:1744-1748.

Hinton, M. A. C. 1926. Monograph of the voles and lemmings (Microtinae) living and extinct. British Museum of Natural History, London, UK.

Hoffmeister, D. F. 1989. Mammals of Illinois. University of Illinois Press, Chicago, Illinois, USA.

Holling. C. S. 1959. Some characteristics of simple types of predation and parasitism. Canadian Entomology 91: 385-398.

-----. 1966. The functional response of invertebrate predators to prey density. Entomological Society of Canada Memoirs 48:1-86.

Holt, R. D., J. Grover, and D. Tilman. 1994. Simple rules for interspecific dominance in systems with exploitative and apparent competition. American Naturalist 144:741-771.

Holzman, S., M. J. Conroy, and J. Pickering. 1992. Home range, movements, and habitat use of coyotes in southcentral Georgia. Journal of Wildlife Management 56:139-146.

Howell, A. B. 1923. Periodic fluctuations in the numbers of small mammals. Journal of Mammalogy 4:149-155.

Hughes, R. N. and M. I. Croy. 1993. An experimental analysis of frequency-dependent predation (switching) in the 15-spined stickleback, *Spinachia spinachia*. Journal of Animal Ecology 62:341-352.

Hughes, T. P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265:1547-1551.

Huston, M. 1979. a general hypothesis of species diversity. American Naturalist 113:81-101.

Jaksic, F. M., J. E. Jimenez, S. A. Castro, and P. Feinsinger. 1992. Numerical and functional response of predators to a long-term decline in mammalian prey at a semi-arid Neotropical site. Oecologia 89:90-101.

Jaksic, F. M., P. L. Meserve, J. R. Gutierrez, and E. Tabilo. 1993. Predation on small mammals in a Chilean semiarid scrub. Revista Chilena de Historia Natural 66:305-321.

James, F. C., and H. H. Shugart, Jr. 1970. A quantitative method of habitat description. Audubon Field Notes 24: 727-736.

Jedrzejewski, W., and B. Jedrzejewska. 1993. Predation on rodents in Bialowieza Primeval Forest, Poland. Ecography:16:47-64.

Johnson, W. E., and W. L. Franklin. 1994. Role of body size in the diets of sympatric gray and culpeo foxes. Journal of Mammalogy 75:163-174.

Kareiva, P. 1994. Space: the final frontier for ecological theory. Ecology: 75:1.

Kaufman, G. A., D. W. Kaufman, and E. J. Finck. 1983. Effects of fire on rodents in tallgrass prairie of the Flint Hills region of eastern Kansas. Prairie Naturalist 15:49-56.

Kaufman, G. A., D. W. Kaufman, and E. J. Finck. 1988. Influence of fire and topography on habitat selection by *Peromyscus maniculatus* and *Reithrodontomys magalotis* in ungrazed tallgrass prairie. Journal of Mammalogy 69:342-352.

Keith, L. B. 1963. Wildlife's ten-year cycle. University of Wisconsin Press, Madison, Wisconsin, USA.

Klett, A. J., T. L. Shaffer, and D. H. Johnson. 1988. Duck nest success in the prairie pothole region. Journal of Wildlife Management 52:431-440.

Korpimäki, E. 1994. Rapid or delayed tracking of multi-annual vole cycles by avian predators? Journal of Animal Ecology 63:619-628.

Korpimäki, E., and K. Norrdahl. 1991. Numerical and functional responses of Kestrels, Short-eared Owls, and Long-eared Owls to vole densities. Ecology 72:814-826.

Korschgen, L. J. 1957. Food habits of the coyote in Missouri. Journal of Wildlife Management 21:424-435.

-----. 1959. Food habits of the red fox in Missouri. Journal of Wildlife Management 23:168-176.

Knable, A. E. 1970. Food habits of the red fox (*Vulpes fulva*) in Union County, Illinois. Transactions of the Illinois Academy of Science 63:359-365.

Korschgen, L. J., and H. B. Stuart. 1972. Twenty years of avian predator-small mammal relationships in Missouri. Journal of Wildlife Management 36:269-282.

Krebs, C. J. 1966. Demographic changes in fluctuating populations of *Microtus californicus*. Ecological Monographs 36:239-273.

Krebs, C. J., B. L. Keller, and R. H. Tamarin. 1969. *Microtus* population biology: demographic changes in fluctuating populations of *Microtus ochrogaster* and *M. pennsylvanicus* in southern Indiana. Ecology 50:587-607.

Lamberson, R. H., B. R. Noon, C. Voss, K. S. McKelvey. 1994. Reserve design for territorial species--the effects of patch size and spacing on the viability of the Northern Spotted Owl. Conservation Biology 8:185-195.

Larter, N. C., A. R. E. Sinclair, and C. C. Gates. 1994. The response of predators to an erupting bison, *Bison bison athabascae*, population. Canadian Field Naturalist 108:318-327.

Lawton, J. H., J. Beddington, and R. Bonser. 1974. Switching in invertebrate predators. Pages 141-158 *in* M. B. Usher and M. H. Williamson, editors. Ecological Stability. Chapman and Hall, London, UK.

Layne, J. N., and W. H. McKeon. 1956. Notes on red fox and gray fox den sites in New York. New York Fish and Game Journal 3:248-249.

Le Boulengé, E. 1987. Package C. M. R.: analysis of capture-recapture data. Universite Catholique de Louvain, Croix du Sud, Belgium.

Linhart, S. B. and F. F. Knowlton. 1975. Determining relative abundance of coyotes by scent station lines. Wildlife Society Bulletin 3:119-124.

Littell, R. C., R. J. Freud, and P. C. Spector. 1991. SAS system for linear models. SAS Institute Incorporated, Cary, North Carolina.

Litvaitis, J. A., and J. H. Shaw. 1980. Coyote movements, habitat use, and food habits in southwestern Oklahoma. Journal of Wildlife Management 44:62-68.

Lord, R. D., Jr. 1958. The importance of juvenile breeding to the annual cottontail crop. Transactions of the Twenty-third North American Wildlife Conference, pp. 269-276.

Lovari, S., P. Valier, and M. R. Lucchi. 1994. Ranging behaviour and activity of red foxes (*Vulpes vulpes*, Mammalia) in relation to environmental variables, in a Mediterranean mixed pinewood. Journal of Zoology 232:323-339.

Lucherini, M., and G. Crema. 1994. Seasonal variation in diet and trophic niche of the red fox in an alpine habitat. Journal of Mammalian Biology 59:1-8.

Lucherini, M., Lovari, S., and G. Crema. 1995. Habitat use and ranging behaviour of the red fox (*Vulpes vulpes*) in a Mediterranean rural area--is shelter availability a key factor? Journal of Zoology 237:577-591.

Lundberg, P. 1988. Functional response of a small mammalian herbivore: the disc equation revisited. Journal of Animal Ecology 57:999-1006.

MacArthur, R. H. and J. W. MacArthur. 1961. On bird species diversity. Ecology 42:594-598.

MacCracken, J. G. 1984. Coyote foods in the Black Hills, South Dakota. Journal of Wildlife Management 48:1420-1423.

Macdonald, D. W. 1981. Resource dispersion and the social organization of the red fox, *Vulpes vulpes*. Pages 918-949 *in* J. A. Chapman and D. Ursley, editors. Proceedings of the Worldwide Furbearer Conference. Frostburg, Maryland, USA.

-----. 1983. The ecology of carnivore social behavior. Nature 301:379-384.

Manly, B. F. J. 1974. A model for certain types of selection experiments. Biometrics 30:281-294.

Manly, B. F. J., P. Miller, and L. M. Cook. 1972. Analysis of a selective predation experiment. American Naturalist 106:719-736.

Martin, E. P. 1956. A population study of the prairie vole (*Microtus ochrogaster*) in northeastern Kansas. University of Kansas Publications, Museum of Natural History 8:361-416.

Meserve, P. L., and B. J. Klatt. 1985. Evidence for noncycling populations and the importance of immigration in voles inhabiting an Illinois tallgrass prairie. American Midland Naturalist 113:255-270.

Messier, F. 1985. Social organization, spatial distribution, and population density of wolves in relation to moose density. Canadian Journal of Zoology 63:1068-1083.

Messier, F., and M. Crete. 1985. Moose-wolf dynamics and the natural regulation of moose populations. Oecologia 65:503-512.

Messenger, P. S. 1968. Bioclimatic studies of the aphid parasite *Praon exsoletum*. I. Effects of temperature on the functional response of females to varying host densities. Canadian Entomologist 100:728-741.

Moehlman, P. D. 1989. Intraspecific variation in canid social systems. Pages 143-163 *in* J. L. Gittleman, editor. Carnivore Behavior, Ecology, and Evolution. Cornell University Press, Ithaca, New York, USA.

Moore, G. C., and G. R. Parker. 1983. Colonization by the eastern coyote (*Canis latrans*). Pages 21-22 *in* A. H. Boer, editor. Ecology and management of the eastern coyote. Wildlife Research Unit, University of New Brunswick, Fredericton, Canada.

Mumford, R. E., and J. O. Whitaker, Jr. 1982. Mammals of Indiana. Indiana University Press, Bloomington, Indiana, USA.

Murdoch, W. W. 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. Ecological Monographs. 39:335-354.

Murdoch, W. M., S. Avery, and M. E. B. Smyth. 1975. Switching in predatory fish. Ecology 56:1094-1105.

Murdoch, W. W., and R. J. Marks. 1973. Predation by Coccinellid beetles: experiments on switching. Ecology 54:160-167.

Murdoch, W. W., and A. Oaten. 1975. Predation and population stability. Advances in Ecological Research 9:2-131.

Murie, A. 1940. Ecology of the coyote in Yellowstone. U.S. National Park Service, Fauna Survey 4:1-206.

Murray, D. L., S. Boutin, and M. O'Donoghue. 1994. Winter habitat selection by lynx and coyotes in relation to snowshoe hare abundance. Canadian Journal of Zoology 72:1444-1451.

Murton, R. K. 1971. The significance of a specific search image in the feeding behavior of the Wood Pigeon. Behavior 40:10-42.

Neimuth, N. D., and M. S. Boyce. 1995. Spatial and temporal patterns of predation of simulated Sage Grouse nests at high and low nest densities--an experimental study. Canadian Journal of Zoology 73:819-825.

Oaten, A., and W. W. Murdoch. 1975. Switching, functional response, and stability in predator-prey systems. American Naturalist 109:299-318.

Ostfeld, R. S., C. G. Jones, and J. O. Wolff. 1996. Of mice and mast: ecological connections in eastern deciduous forests. BioScience 46:323-330.

Ozoga, J. J., C. S. Bienz, and L. J. Verme. 1982. Red fox feeding habits in relation to fawn mortality. Journal of Wildlife Management 46:242-243.

Ozoga, J. J., and E. M. Harger. 1966. Winter activities and feeding habits of northern Michigan coyotes. Journal of Wildlife Management 30:809-818.

Patalano, M., and S. Lovari. 1993. Food habits and trophic niche overlap of the wolf (*Canis lupus*, L. 1758) and the red fox (*Vulpes vulpes*, L. 1758) in a Mediterranean mountain area. Revue d' Ecologie la Terre et la vie. 1993 48:279-294.

Pearson, O. P. 1966. The prey of carnivores during one cycle mouse abundance. Journal of Animal Ecology 35:217-233.

-----. 1971. Additional measurements of the impact of carnivores on California voles (*Microtus californicus*). Journal of Mammalogy 52:41-49.

Person, D. K., and H. H. Hirth. 1991. Home range and habitat use of coyotes in a farm region of Vermont. Journal of Wildlife Management 55:433-441.

Phillips, M. K. and G. F. Hubert, Jr. 1980. Winter food habits of coyotes in southeastern Illinois. Transactions of the Illinois State Academy of Science 73:80-85.

Piersma, T. J. Vangils, P. Degoeij, and J. Vandermeer. 1995. Holling's functional response model as a tool to link the food-finding mechanism of a probing shorebird with its spatial distribution. Journal of Animal Ecology 64:493-504.

Poulle, M. L., M. Artois, and J. J. Roeder. 1994. Dynamics of spatial relationships among members of a fox group (*Vulpes vulpes*, Mammalia, Carnivora). Journal of Zoology 233:93-106.

Priest, J. M. 1986. Some aspects of the ecology of the coyote: Dixon Springs Agricultural Center, S. E. Illinois. Ph.D. Thesis. Southern Illinois University, Carbondale.

Reice, S. R. 1985. Experimental disturbance and the maintenance of species diversity in a stream community. Oecologia 67:90-97.

Richens, V. B., and R. D. Hugie. 1974. Distribution, taxonomic status, and characteristics of coyotes in Maine. Journal of Wildlife Management 38:447-454.

Roughton, R. D., and M. W. Sweeny. 1982. Refinements in scent station methodology for assessing trends in carnivore populations. Journal of Wildlife Management 46:217-229.

Sale, P. 1977. Maintenance of high diversity in coral reef fish communities. American Naturalist 111:337-359.

Sargeant, A. B., and S. H. Allen. 1989. Observed interactions between coyotes and red foxes. Journal of Mammalogy 70:631-633.

Sargeant, A. B., S. H. Allen, and J. O. Hastings. 1987. Spatial relations between sympatric coyotes and red foxes in North Dakota. Journal of Wildlife Management 51:285-293.

SAS Institute, Inc. 1990a. SAS/STAT User's Guide, Version 6, Fourth Edition, Volume 2, Cary, North Carolina, USA.

SAS Institute, Inc. 1990b. SAS/STAT User's Guide, Version 6, Fourth Edition, Volume 1, Cary, North Carolina, USA.

Schramm, P. and B. J. Willcutts. 1983. Habitat selection of small mammals in burned and unburned tallgrass prairie. Pages 49-55 *in* R. Brewer, editor. Proceedings of the 8th North American Prairie Conference. Western Michigan University Printing, Kalamazoo, Michigan, USA.

Schueler, R. L. 1951. Red fox food habits in a wilderness area. Journal of Mammalogy 32:462-464.

Scott, T. G. 1943. Some food coactions of the northern plains red fox. Ecological Monographs 13:427-479.

Scott, T. G.. and W. D. Klimstra. 1955. Red foxes and a declining prey population. Southern Illinois University, Monograph Series No. 1. 123 pp.

Sheldon, J. W. 1992. Wild dogs: the natural history of the nondomestic Canidae. Academic Press, Inc., San Diego, California, USA.

Shivik, J. A., and R. L. Crabtree. 1995. Coyote activity levels in relation to presence of California Gulls at Mono Lake, California. California Fish and Game 81:22-28.

Sillerozubiri, C., and D. Gottelli. 1995. Spatial organization in the Ethiopian wolf, *Canis simensis*--large packs and small stable home ranges. Journal of Zoology 237:65-81.

Sillerozubiri, C., F. H. Tattersall, D. W. MacDonald. 1995. Habitat selection and daily activity of giant molerats (*Tachyoryctes macrocephalus*)--significance to the Ethiopian wolf (*Canis simensis*) in the afroalpine ecosystem. Biological Conservation 72:77-84.

Smallwood, K. S. 1995. Scaling Swainson's Hawk population density for assessing habitat use across and agricultural landscape. Journal of Raptor Research 29:172-178.

Solomon, M. E. 1949. The natural control of animal populations. Journal of Animal Ecology 18:1-35.

Soluk, D. A. 1993. Multiple predator effects--predicting combined functional responses of stream fish and invertebrate predators. Ecology 74:219-225.

Sperry, C. C. 1941. Food habits of the coyote. U. S. Fish and Wildlife Service Research Bulletin No. 4.

Storch, I. 1993. Patterns and Strategies of winter habitat selection in alpine Capercaillie. Ecography 16:351-359.

Todd. A. W., L. B. Keith, C. A. Fischer. 1981. Population ecology of coyotes during a fluctuation of snowshoe hares. Journal of Wildlife Management 45:629-640.

Voight, D. R., and B. D. Earle. 1983. Avoidance of coyotes by red fox families. Journal of Wildlife Management 47:852-857.

Ward, D., and D. Saltz. 1994. Foraging at different spatial scales: dorcas gazelles foraging for lilies in the Negev desert. Ecology 75:48-58.

Warner, R. E. 1994. Agricultural land use and grassland habitat in Illinois--future shock for midwestern birds. Conservation Biology 8:147-156.

Weaver, J. L., and S. W. Hoffman. 1979. Differential delectability of rodents in coyote scats. Journal of Wildlife Management 43:783-786.

Wolff, J. O. 1996. Population fluctuations of mast-eating rodents are correlated with acorn production. Journal of Mammalogy, in press.

Woolf, A., D. R. Shoemaker, and M. Cooper. 1993. Evidence of tularemia regulating a semi-isolated cottontail rabbit population. Journal of Wildlife Management 57:144-157.

Yunger, J. A. 1996. Predation, competition, and abiotic disturbance: population dynamics of small mammals. Ph.D. Dissertation. Northern Illinois University.

Zabel, C. J., and S. J. Taggart. 1989. Shift in red fox, *Vulpes vulpes*, mating system associated with El Niño in the Bering Sea. Animal Behavior 38:830-838.