ABSTRACT

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ABSTRACT

Predation and food availability have been implicated in annual non-cyclic fluctuations of vertebrate prey at mid-latitudes. The timing and magnitude of these factors are unclear due to a lack of large-scale field experiments, little attention to interactions, and a failure to closely link vertebrate predators with their prey. From October 1992 to January 1996, small mammal populations were censused on eight 0.6 ha plots at monthly intervals in a 32-ha prairie restoration at Fermi National Accelerator Laboratory, Illinois. Terrestrial vertebrate predators were excluded after July 1993 from four of the eight plots and canid diets monitored. Both terrestrial and avian vertebrate predators were excluded in March 1994. During 1993 small mammal densities (i.e., Microtus pennsylvanicus, Peromyscus leucopus, and P. maniculatus) were relatively high. Following peak densities in late summer, Microtus numbers were 2-3x greater on exclusion plots relative to controls due to preferential selection of Microtus by canids, as reflected in diets. Following an ice-storm and crash in small mammal numbers (particularly Microtus), vertebrate predator exclusion had no detectable effect on P. leucopus numbers, probably due to an abundance of alternative prey (i.e., Sylvilagus floridanus). Meadow vole numbers began to increase in Fall 1995, and a numerical effect of predator exclusion, similar to that in 1993, was observed. Predator exclusion had no detectable effect on the movements and spatial

patterns of Microtus during 1993. There was a significant decrease in home range and a significant increase in home range overlap for P. leucopus on the predator exclusion plots. The change in spatial behavior may be due to interspecific competition with Microtus resulting from increased densities on exclusion plots. Thus, predators had an indirect effect on P. leucopus spatial patterns mediated through M. pennsylvanicus. The role of food limitation was studied using natural and manipulative experiments. Unusually high acorn production in Fall 1994 resulted in increased P. leucopus numbers at one Fermilab site due to immigration since survivorship or reproduction were unaffected. A food supplementation experiment during October 1994-March 1995 induced a strong increase in P. leucopus numbers, due again to immigration, although reproduction also was advanced by two months.

NORTHERN ILLINOIS UNIVERSITY

PREDATION, COMPETITION, AND ABIOTIC DISTURBANCE: POPULATION DYNAMICS OF SMALL MAMMALS

A DISSERTATION SUBMITTED TO THE GRADUATE SCHOOL IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE DOCTOR OF PHILOSOPHY

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CHAPTER 1

WHAT DETERMINES DEMOGRAPHIC FLUCTUATIONS IN SMALL MAMMALS? A REVIEW

Introduction

Plagues, or periodic eruptions in small mammal densities, are mentioned in the earliest records of humankind. In the 13th century A.D. government officials in Europe (primarily France) began keeping records of plague years. However, up through the 19th century there were no published records of periodicity or regular fluctuations in the number of small mammals (Elton 1942). Based on fur returns, Seton (1912) used the records of the Hudson's Bay Company to document what he described as the 10-year cycle of the vertebrate predators of the boreal forest of North America. Elton (1924) subsequently described a 10-year cycle for boreal forest hares, a 3- to 4-year cycle for arctic vertebrate predators and their prey, and a 3- to 4-year cycle for small mammals in other parts of Europe and the United States. A half century after Elton's (1924) ground breaking work on the causes of small mammal cycles, Krebs and Myers (1974) published their monographic review, "Population cycles in small mammals." Also around this time, some of the first field experiments on small mammal population ecology were published (Grant 1969, 1971). These experiments not only added a new approach to studying small mammal fluctuations,

but also placed a greater emphasis on biotic interactions. Although scientific study is a continuous, on-going process, Elton's (1924) seminal investigation and Krebs and Meyer's (1974) synthesis in the early 1970s provide a good frame of reference for which to review the "early" history of small mammal population ecology.

The mid-1970s saw a proliferation of ecological research. For example, between 1970 and 1974 the journal Ecology published an average of 1275.4 (±68.78SE) pages per year; between 1990-1994 an average of 2427.2 (±34.62SE) pages were published per year, a nearly two-fold increase. In addition to the increased volume of existing journals, several new ecological journals have appeared (e.g., Ecological Applications, Holarctic Ecology, Journal of Chemical Ecology, Functional Ecology, Evolutionary Ecology, Ecological Engineering). Between 1970 and 1994 there was a three-fold increase in the number of papers presented at the Annual Meeting of the American Society of Mammalogists, a significant portion of which pertained to small mammal ecology. The proliferation of ecological research, increased emphasis on biotic interactions, and the recognition of the importance of field experiments in the early 1970s provides a convenient time period over which to review the "recent" work on small mammal population ecology over roughly the past 25 years.

The First Half Century: 1924-1974

The significance of Elton's (1924) seminal work on mammalian population dynamics is that he not only described putative cycles but attempted to determine

causation. It had recently been shown that changes in climate were correlated with the 11.1-year cycle of sunspot activity (Walker 1923). Elton concluded that the 10-year wildlife cycle was the result of sunspot activity and the subsequent climatic fluctuations. In order to reconcile the 10-year cycle suggested for mammalian populations and the 11.1 year cycle of sunspot activity, Elton developed several explanations to account for the discrepancies in the maxima and minima of vertebrate numbers and sunspots. For the 3- to 4-year (average 3.6 y) cycle, common in Europe, at mid-latitudes in North America, and among microtines in general, Elton concluded that populations would undergo "regular" increases in numbers. Following a Malthusian perspective, once populations reached a certain threshold, disease and epidemic would cause a rapid decrease in numbers. This pattern repeated itself at regular intervals causing cycles. He also suggested that the 3- to 4-year cycle could be overlaid on the 10-year cycle, again due to sunspot activity. It was assumed that the large discrepancy in the intrinsic rate of increase between vertebrate prey and their predators precluded any significant numerical effect on small mammal populations. There was limited discussion on the role of food availability in limiting numbers, although in general the topic received relatively little attention. It should also be recognized that implicit in Elton's work is some form of dynamic equilibrium and density-dependence. This "balance of nature" approach philosophy throughout his extensive writings (Elton 1927, 1939, 1942, 1966).

The influence of sunspots on the dynamics of animal and plant populations culminated in the Matamek Conference (Huntington 1931). A general conclusion of

the conference was that numerous cyclic populations were controlled by, although not necessarily caused by, outside forces dominating all forms of life. A probable outside force was solar activity, manifested as sunspots. At the time of the Matamek Conference, Leopold (1931) published a paper showing that grouse cycles in Britain and North America were not synchronous. He concluded that this precluded a "global" effect of sunspots. A subsequent, rigorous analysis showed that vertebrate population cycles and sunspots were not significantly correlated (MacLulich 1937). The sunspot cycles averaged 11.1 years whereas the vertebrate predator-prey cycle averaged 9.7 years. Thus, by the late 1930s the solar hypothesis was largely put to rest and attention turned primarily to food availability (Elton 1939, Hamilton 1939).

However, Hamilton (1939) was a strong opponent of the balance of nature concept, contrary to Elton (1939). He put forth the widespread variability in mammalian species numbers as evidence that "...living organisms in a stable equilibrium is nothing more than fiction" (p. 262). This set the stage for not only what causes observed population dynamics in small mammals, but also a more simple question: what, if any, is the pattern of fluctuation?

Starting in the late 1920s and continuing into the early 1940s, several investigators attempted to document epizootic agents responsible for crashes in small mammal populations. In northern California, Bacillus marisepticus was found to be the causative agent of mouse septicemia, and was presumed to be responsible for the large scale die-off of microtines (Wayson 1927). In Scotland, Findlay and Middleton (1934) were able to document the occurrence of Toxoplasma cysts in the brains of

field voles (Microtus agrestis). Based on the presence of the cysts and observed nervous disorders, they concluded that the Toxoplasma was probably responsible for a crash in vole numbers. Working with meadow voles (Microtus pennsylvanicus) in central New York, Hamilton (1937) observed symptoms similar to those documented by Findlay and Middleton, leading him to conclude that disease was responsible for a crash in vole densities. Numerous other infectious and/or communicable diseases were suggested to cause population declines in lagomorphs and rodents (e.g., Francisella tularensis, Bacillus murisepticus, Bacterium pitymtsi; Elton 1942). However, it should be recognized that during this time, several other investigators studied crashes in small mammal numbers but were unable to document any epizootic events (Elton et al. 1931, Elton 1942).

An interesting discovery, which has received relatively little attention in recent years, is what Green and Larson (1938a, 1938b) referred to as shock disease. Shock disease, first documented in snowshoe hares (Lepus americanus), results from extremely low carbohydrate reserves in the liver. Even low levels of excitement, stress, or exertion results in the rapid depletion of glycogen reserves and subsequent blood sugar levels 30 to 275 times below average. The low blood sugar results in individuals going into hypoglycemic shock, comas, and subsequently death. Field observations corroborated the laboratory findings.

Following World War II, there was a renewed interest in small mammal population ecology. Christian (1950, 1955, 1961, Christian and Davis 1964) produced a series of influential papers on the physiological aspects of small mammal population

fluctuations. Christian's (1950) first contribution summarized the existing literature, drew general conclusions, and formulated a new theory. The summary included studies on small mammal fluctuations and the factors thought to be responsible for numerical declines. Up to that time, causal factors were assumed to be diseases and epizootics. However, Christian concluded that there was little support for the epizootic hypothesis, citing studies that could not document the presence of infectious disease (see Elton 1942). He also argued that most investigators did not provide adequate support for the proposition that the presence of disease caused population declines. The one exception to this was shock disease. Based on pre- and postmortem descriptions of several species during population crashes, Christian concluded that shock disease was one underlying mechanism that may have been responsible for population crashes among small mammals. Christian's theory was largely an extension of Selye's general adaptation syndrome (1946). High population densities resulted in increased pituitary-adrenocortical activity and inhibition of reproductive functions. In addition, it was suggested that increased pituitary-adrenocortical secretions indirectly caused increased mortality through decreased resistance to disease, parasites, and environmental stress.

Numerous studies went on to document a wide array of physiologically detrimental effects that could potentially reduce population density, including: increased intrauterine mortality (Myers and Poole 1962); increased reabsorbtion of embryos (Helmreich 1960); increased infant mortality (Chance 1956); permanent behavioral disorder of young conceived by mother subjected to high densities (Keely

1962); and increased susceptibility to myxomatosis (Myktowycz 1961). Accumulating evidence led Christian and Davis (1964) to conclude that behavioral-endocrine feedback systems were important in regulating rodent and lagomorph populations in a density-dependent fashion. They reiterated Milne's (1961) assertion that environmental factors, such as disease, food, and predation, may at times limit population growth, but that physiological regulation was the predominant force. However, nearly all previous tests of Christian's hypothesis were carried out in cages with extremely high densities of laboratory mice, rats, and rabbits. One attempt to test Christian's hypothesis in the field (Krebs 1964) met with several methodological difficulties (Christian and Davis 1964) and equivocal results (Colinvaux 1973).

Similar to Christian, Chitty (1960) concluded that, in general, there was inadequate evidence to support the role of disease, food, and predation in limiting small mammal population growth. In addition, he went on to discount shock disease and Christian's adrenopituitary hypothesis. He discussed (but did not cite) a study with wild voles and concluded that "No evidence was discovered to suggest that any of them has a pathological condition that impaired their ability to store glycogen" (p. 104). He also argued that the laboratory data for Lepus americanus are "...not only unjustified, but are actually contradicted by the field evidence" (p. 104). Chitty asserted that results supporting shock disease in the common vole (Microtus arvalis; Frank 1957) applied only to ill-treated animals in captivity. He cited several additional investigations (Green and Evans 1940, Clarke 1955, Godfrey 1955) presenting data he believed did not support Christian's hypothesis.

Chitty also developed a population dynamics model based on an intrinsic regulatory mechanism (Chitty 1952, 1958, 1960, 1967), working independently of Christian (Crowcroft 1991). His model assumed a genetically based behavioral polymorphism. During a population decline, there would be selective pressure for aggressive individuals. The aggressive individuals had reduced fecundity, as compared to more submissive individuals. This was the result of the aggressive individuals spending a greater amount of time defending territories and being engaged in antagonistic interactions. In addition, the aggressive behavior resulted in increased spacing between individuals, further exacerbating the decline in numbers. However, since the individuals with the aggressive phenotype had a greater probability of surviving the crash and subsequently reproducing, there was a selective basis for their behavior. Following the crash in density, social interactions were greatly reduced and offspring of individuals that had survived through the crash would begin to reproduce. Also, highly aggressive individuals should have lower reproductive rates as densities decline. Young expressing the more subordinate behavior, yet with higher fecundity, would contribute more to the increase in population size.

Chitty cited a variety of laboratory and field observations from the 1950s and 1960s as support for his hypothesis (Chitty 1960, 1967, 1970), primarily differences in the survivorship and behavior of voles during the expanding, peak, and declining populations. However, it was not until the development of electrophoretic techniques in the late 1950s and early 1960s that it became possible to test for a genetic difference in individuals during population fluctuations. The first studies began to appear in the

late 1960s; for purposes of continuity, they will be discussed in the section "The Past Quarter Century."

The emphasis on intrinsic regulation was further accentuated by a view of predator-prey interactions that developed throughout the 1950s, largely owing to Errington (1946, 1963). Prior to 1970 there were no experiments on the effects of vertebrate predators on prey populations, although several investigators carried out observational studies. These ranged from attempts to carefully quantify the abundance of prey and the number of prey consumed to anecdotal impressions (Errington 1946, Gross 1947, Chitty 1952, Lockie 1955, Craighead and Craighead 1956, Watson 1957, Pitelka 1958, Krebs 1964). Errington believed that predators generally took only "surplus" prey and had little or no effect on prey density. He strongly emphasized density compensation. That is, even though predators were observed to regularly capture individuals (small mammals included), the prey replaced themselves at such a rate as to preclude any numerical effects. The Erringtonian perspective continued throughout most of the 1960s (Lidicker 1994). However, by the late 1960s to early 1970s the MacArthunian influence (MacArthur 1972) of biotic interactions (i.e., competition) and Paine's (1966) work on predation in intertidal zones started to take root. The idea that predators played little or no role in determining small mammal numbers started to fall from favor.

Contrary to the pre-1970s prevailing view of negligible predation effects on small mammal populations, was the work of Thompson (1955), Pitelka et al. (1955), and Pearson (1964). Thompson (1955) concluded that predators were important in

causing the decline of the brown lemming (Lemmus trimucronatus = L. sibiricus), and least weasels (Mustela nivalis), specifically, were responsible for accentuating the low phase. Working near Barrow, Alaska, Pitelka et al. (1955) investigated the interaction between avian predators and L. sibiricus. They concluded that predators were able to depress lemming densities during the increasing phase of the cycle, resulting in protracted numerical responses and dampened fluctuations. Pearson (1964) used live-trapping to estimate small mammal densities and scat analysis to estimate prey consumed in a 14.2-ha California grassland. He concluded that in less than one year, predators consumed 88% of the California voles (Microtus californicus), 33% of the western harvest mice (Reithrodontomys megalotis), and 7% of the house mice (Mus musculus). Although the methods used in the study resulted in a potentially large sampling error, his work provided support that vertebrate predators are able to depress vole numbers.

Prior to 1970, a limited number of experiments were also directed at the role of food availability in regulating small mammal densities (Baumgartner 1938, Hoffmann 1958, Lord and Casteel 1960, Marsh 1962, Krebs and DeLong 1965, DeLong 1967). Several of the experiments incorporated design problems, such as supplemental food of low nutrient value (Batzli and Pitelka 1971) and plants which did not respond to fertilization (Krebs and Myers 1974). However, in some instances, results did suggest that food may play a role in determining small mammal numbers (Bendell 1959, Schultz 1969). Bendell (1959) introduced P. leucopus to an island off the coast of British Columbia. Prior to food supplementation, the population failed; following a

second introduction and the addition of food, mouse densities increased and were in excess of a reference island and the mainland. The supplemental food had the greatest effect on mortality. By fertilizing a 2.4-ha field, Schultz (1969) was able to increase primary productivity 3- to 4-fold and protein content of the vegetation 4- to 5-fold. Following a year of relatively high densities, lemming numbers rapidly declined during the winter on a control plot, while the decline was more protracted on the fertilized plot.

Somewhat out of the mainstream of small mammal population ecology, yet highly relevant to population ecology as a whole, were the theses of Wynne-Edwards (1962) and Lack (1954a). Although Wynne-Edwards' work was never strictly applied to small mammal population ecology, it was significant in that it epitomized the intrinsic self-regulation view. He used a density-dependent approach, assuming populations were homeostatic. That is, populations would regulate themselves below a particular threshold that ensured continuous food availability. This obviously required a natural-selection to operate at the group level, which was highly controversial (Wiens 1966), and Wynne-Edwards' hypothesis fell quickly from favor.

Lack (1954a), an ornithologist, used largely bird examples to support his food limitation hypothesis. Lack assumed that populations were directly limited by food availability and that individuals would simply starve if densities exceeded the food supply. During the late 1950s and 1960s small mammal ecologists chose instead to focus on intrinsic regulatory mechanisms. In general, food availability received relatively little attention and was considered of only minor importance. However, as

illustrated by the proliferation of food supplementation studies described below (The Past Quarter Century), ultimately Lack's hypothesis had a strong influence on small mammal population ecology.

The early 1950s saw not only renewed interest in what causes fluctuations in small mammal populations, but also the pattern of fluctuation. Clarke (1949) concluded that small mammal populations generally undergo regular 3- to 4-year cycles. Christian (1950) even went as far as to say, "The number of species now known to cycle are legion, in fact the non-cyclic mammal is the exception rather than the rule" (p 257). The following year, in a text on wildlife management, Gabrielson (1951) attacked the idea that mammalian populations were in some type of "natural balance." By comparing existing time series of vertebrate population dynamics with Tippett's (1927) "random sampling numbers", Cole (1951) concluded that several previously purported cycles were simply random fluctuations. The paper was so controversial that it prompted the editor of the Journal of Wildlife Management, O. H. Hewitt, to invite recognized authorities to a symposium (Hewitt 1954). Ten papers from the symposium were subsequently published as a special issue of The Journal of Wildlife Management (volume 18, no. 1). Results of the symposium were far from conclusive (see, for example, Cole 1954, Hutchinson 1954, Lack 1954b, Marshall 1954), and the debate continued as to whether fluctuations in small mammal numbers were truly cyclic with regular fluctuations or simply random processes.

The debate become even more pronounced with the publication of Andrewartha and Birch's (1954) seminal volume. Working with invertebrates, Andrewartha and

Birch assumed that populations fluctuated independent of density and provided mathematical models to support their theory. Their approach was in direct contradiction to the earlier work of Nicholson and Bailey (1935), who, also working with invertebrates, formulated density-dependent equations. By the early 1970s, the density-dependent approach had largely "won-out" and it was generally assumed systems were in some form of equilibrium (MacArthur 1972). This included the regulation of animal population dynamics in general (McLaren 1971), and, more specifically, small mammals. The emphasis placed on cyclic fluctuations of small mammals is reflected in Elton's last text on animal ecology: "All small rodents, in all parts of the world for which there are any data, undergo periodic fluctuations of the order of three or four years. Wild rats, mice hamsters, mouse-hares, gerbils, etc., all appear to have this as their regular mechanism of number-regulation. The general fact has been noticed in a dozen different countries, e.g. England, Scandinavia, Central Europe, France, Italy, Palestine, Siberia, Brazil, and India. The large rodents also undergo similar fluctuations in which epidemics play an important part" (Elton 1966, p. 135). Krebs and Myers (1974) went on to state that: "We conclude that microtine rodent populations normally undergo population cycles with a period of three to four years and this density pattern should be assumed to be the normal configuration. We feel that the burden of proof should be shifted to those who would claim to have a non-cyclic population" (p. 278). The stage was set for a vigorous debate on not only how small mammal populations fluctuate, but what causes the observed fluctuations, particularly intrinsic versus extrinsic forces.

The Past Quarter Century

Intrinsic Regulation

Genetic Polymorphism

Theory. Myers and Krebs (1974) expanded upon the Chitty hypothesis by including dispersal. They assumed that the less aggressive individuals with a high reproductive rate also had a propensity for dispersal during the increase phase of a cycle. This would result in a greater proportion of the individuals during the peak and decline phase being aggressive and having a relatively low reproductive potential.

The model was subsequently modified to include kin-selection (Charnov and Finerty 1980). At a population low it was assumed that individuals interacting within their neighborhood (*sensu* Hamilton 1972) were closely related and, i.e., would have a high coefficient of relatedness. As densities increase dispersal becomes more important and the coefficient of relatedness decreases. Associated with the decrease in relatedness was an increase in aggression. The relatively high levels of aggression would in turn lead to greater dispersion between individuals and a subsequent decrease in density. Following the decline in numbers, the rate of dispersal would decline and kin groups become reestablished. Kin groups would have the highest reproduction and survival, leading to an increase in population density.

Several other models have been developed along lines similar to the Chitty hypothesis. That is, variations in aggressive behavior, reproductive potential, and the propensity to disperse are assumed to drive small mammal population fluctuations. However, these studies rely primarily on dispersal, not on the fluctuating genetic composition of the population, and will be discussed in the subsequent section.

Empirical Evidence. Shortly following the development of electrophoretic techniques, investigators began to look for genetic polymorphisms that correlated with observed behavioral polymorphisms. That is, was there evidence for a genetic basis of the Chitty hypothesis? Changes in gene frequency have been found to be associated with demographic fluctuation of *M. agrestis* (Semeonoff and Robertson 1968), *M. pennsylvanicus*, prairie voles (*Microtus ochrogaster*) (Tamarin and Krebs 1969), and beach voles (*Microtus breweri*) (Kohn and Tamarin 1978). Canham (1969) demonstrated that the population density of deer mice (*Peromyscus maniculatus*), northern red-backed voles (*Cleithrionomys rutilus*), and southern red-backed voles (*Cleithrionomys gapperi*) was positively correlated with heterozygote fitness. By simultaneously monitoring changes in fitness, gene frequencies, and population density, Gaines and Krebs (1971) found a significant correlation between gene frequency and density. During the increase phase, survival was relatively high and gene frequencies changed in favor of a genotype with relatively high reproductive success; during the decline phase, survivorship was relatively low and gene frequencies changed in favor of genotypes with relatively low reproductive success.

A majority of the previous studies relied on either the tranferrin (*Tf*) and/or leucine aminopeptidase (*Lap*) electromorphs as genetic markers (Canham 1969, Tamarin and Krebs 1969, Gaines and Krebs 1971, Kohn and Tamarin 1978). This was subsequently expanded upon using M. ochrogaster to include an additional three loci (Gaines et al. 1978). Correlations between the additional three loci and population density were equivocal. The use of the *Tf* and *Lap* electromorphs as reliable genetic markers was subsequently questioned due primarily to differential binding with sialic acid residues (McGovern and Tracy 1981). However, subsequent work suggested that the two electromorphs were reliable genetic markers (Mihok and Ewing 1983, Gaines and Gorman 1985).

Empirical investigations testing the Chitty hypothesis provide support for a correlation between fluctuating densities and genetic polymorphisms in small mammals (Gaines 1981). However, correlation does not indicate a causal relationship. Disentangling behavioral traits, which are probably coded by several loci and may or may not be linked, is at best difficult. It is also possible that the changes in demography may be causing the fluctuations in allele frequency. That is, a mechanism(s) other than the behavioral polymorphism could be driving population fluctuations, and in turn cause the allelic fluctuations.

More recent attempts to test the Chitty hypothesis have relied on numerical simulations. Warkowska-Dratnal and Stenseth (1985) were able to generate damped oscillations. However, to do so their model required the inclusion of an additional assumption: "smart lemmings," dispersing individuals that only enter occupied habitat

patches when unoccupied ones are unavailable. Subsequent attempts to produce more parsimonious models were unsuccessful (Stenseth and Lomnicki 1990), leading the investigators to conclude that: "... the hypothesis proposed by Charnov and Finerty (1980) is not a plausible one for explaining the regular density cycles seen in several small rodent populations" and that because "... the Chitty hypothesis for explaining the microtine density cycle is implausible, we are forced to conclude that this class of intrinsic hypotheses (represented by the Chitty and Charnov-Finerty hypotheses) seems unable to account for the microtine density cycles" (p. 237). Stenseth and Lomnicki (1990) articulated the need for a greater emphasis on extrinsic factors, possibly coupled with intrinsic factors, to explain small mammal fluctuations. Although some students of small mammal population ecology still support the Chitty hypothesis as an explanation for microtine cycles, rigorous support remains elusive (Stenseth 1995).

Physiological and Reproductive Inhibition

Reproductive inhibition may set limits of maximum densities. If reproductive output is physiologically constrained, as has been suggested for some mammals, females can increase their relative fitness by reducing the fitness of other females (Haigh 1987). There is evidence to suggest that reproductive inhibition may play a role in regulating animal populations in general, and small mammal populations in particular (Haigh 1987), including Peromyscus spp. Laboratory studies of P. eremicus (Skryja 1978), P. maniculatus (Terman 1968, 1979, 1980), and P. leucopus (Haigh 1983a, 1983b, 1987) have demonstrated reproductive inhibition of young females by

adult females. Nearly complete reproductive inhibition in young females was reported for the duration (150-300 days) of several of these studies. If exposure to adult females was terminated, average recovery time until young females became pregnant was 49 days (Haigh 1987). The reproductive inhibition has generally been attributed to chemosignals (Terman 1968, Haigh 1987), though tactile cues may also be important (Terman 1979). Vandenbergh (1987) and Schadler (1990) found similar results for house mice (Mus musculus) and pine voles (Microtus pinetorum), respectively. However, the previous investigations have all been conducted under laboratory conditions that simulate high densities, confined quarters, and/or close proximity. The results need to be confirmed through field investigations.

Territoriality and Home Range

Theory. There are several models that make qualitative predictions about home range size based on resource availability (Cody 1974, Ebersole 1980, Schoener 1983). Not all of these models attempt to relate home ranges or territories to population density. However, since it is often accepted that changes in home range size lead to changes in dispersion and ultimately density, it is useful to provide a brief review on resource territory models. Early theories of territoriality were based on the intuitively appealing concept that as food availability increases, territory size should decrease and vice versa (review by Ricklefs 1973 and Brown 1975). This can be defined by the equation $E = pA$, were E = energy, p = food availability, and A = area of territory (home range). It can be seen that as p increases, A can decrease while E remains

constant. Ebersole (1980), however, pointed out that there can be selective pressure not only to obtain necessary energy but also to maximize energy intake. The energy obtained beyond the requirements for basic body maintenance, growth, and reproduction can be directed to reduced intervals between reproductive bouts, increased litter/clutch size, increased growth rates so that reproductive maturity is attained at an early age and/or large body size that aids in the probability of obtaining a mate(s).

Although territory size may increase with food availability (specifically, in a linear fashion [Cody 1974]), there are, obviously, limitations. Schoener (1983) modeled the limitation as energy constraints, $E = pA - f(A_e)$ (eq. 1) where A_e is a simple energetic cost function based on area; the function has been shown to be a positively accelerating slope. The constraints result from the increased energy required for traversing a large territory and defense against intruders. As A increases so does the perimeter, contact with surrounding territories, and the probability of intrusion. The optimal territory size, $\hat{A}$, that maximizes E can be calculated by equating the derivative of equation (1) with respect to A to zero (see Ebersole 1980 for a more detailed account of the calculations). Thus, it is possible to determine the expected influence of food availability on territory size. Equation (1) has the disadvantage that individuals may be operating under constraints other than energetic, specifically predation and injuries due to antagonistic interactions. As previously discussed, an increase in A is accompanied by increased movements. This increase in activity leads to a greater probability of being detected and captured by a predator, obviously

resulting in a significant decrease in fitness. Thus, by modifying equation (1) so that fitness, F, replaced E, parameters other than energetics can be included. Equation (1) then becomes $F = pA - f(A_c)$ (eq. 2) where $f(A_c)$ is a complex function incorporating different fitness costs. Equation (2) has the additional advantage that by using F as the currency, the model is placed in the broader theoretical framework of natural selection. If the theory is supported, that is individuals have an optimal territory size, then $A \approx \hat{A}$. Cooper (1978) developed a model in which home range size varied as a nonlinear function of density. The nonlinearity was due to variation in home range overlaps between individuals. Cooper (1978) assumed that as density increased so did the aggressiveness of individuals, which in turn reduces home range overlap and ultimately home range size.

Ostfeld (1985, 1990) has developed a model which predicts the occurrence of territoriality on microtine rodents, though the model may be applied to small mammals in general. Three predictions culminate from the model: (1) Territoriality in females should be food-based, but in males female-based. This is based on the premise that females expend a greater proportion of energy on the rearing of offspring than males and thus require a larger food supply. (2) Patchily distributed foods (a dependable resource) and/or slowly renewing foods (a valuable resource) should result in territorial females; evenly distributed foods (difficult to defend) that are quickly renewed (less valuable resource) should result in nonterritorial females. (3) When females are territorial, males should be nonterritorial; when females are nonterritorial males should be territorial. This third prediction assumes that essentially females are

the limiting resource for males; males adjust territories and/or home ranges in response to female availability.

Empirical Evidence. Home range size has been shown to be inversely related to population density for M. pennsylvanicus and M. ochrogaster inhabiting grasslands (Van Vleck 1969, Krebs 1970) and M. pennsylvanicus in marsh habitat (Getz 1961). Similarly, as density increased, home range size decreased, in desert populations of long-tailed pocket mice (Perognathus formosus), little pocket mice (Perognathus longimembris), Merriam's kangaroo rat (Dipodomys merriami), and chisel-toothed kangaroo rat (Dipodomys microps; Maza et al. 1973). Alternatively, working in a central California grassland, Batzli (1968) concluded that home range size in M. californicus was independent of density. The absence of an association between population size and home range size was also reported for eastern chipmunks (Tamias striatus) in a Pennsylvania deciduous forest (Mares et al. 1980). In southwestern Argentina, Contreras (1972), found that the annual home range size of the long-tailed pygmy rice rat (Oryzomys [=Oligoryzomys] longicaudatus) remained relatively constant, regardless of density. However, as density increased so did home range overlap between females. Under a wide range of densities there was relatively little change in female home range size of Japanese field voles (Microtus montebelli) on Kyushu, Japan. Male home range size, however, increased substantially during low densities (Arai and Shiraishi 1982).

Abramsky and Tracy (1980) and Gaines and Johnson (1982) were the first to emphasis a causal relationship between home range and density. Both studies used M.

ochrogaster, placed an emphasis on dispersal, and used home range length as opposed to area. Abramsky and Tracy (1980) found a significant negative, linear correlation between the length of home range and population density. An almost three-fold decrease in home range length occurred as density increased from 10 to 90 individuals per ha. The investigators concluded that antagonistic encounters between M. ochrogaster increased as a function of density; the increase in intraspecific interactions resulted in decreased home range size and a probable increase in emigration. There was also a negative, linear association between home range size and density of M. ochrogaster adult females in an eastern Kansas grassland (Gaines and Johnson 1982). However, there was no correlation between home range size and density for other age classes. For both adult and subadult males, there was a positive linear association between dispersal rate and home range size. However, a stepwise regression indicated that home range may be correlated with several other environmental and demographic variables, suggesting a relatively complex relationship.

The previous studies provide only limited support for density-home range theoretical models: under certain conditions there is an inverse relationship between home range size and population density. However, there is also empirical support for territoriality models and resource based home range sizes. Although there are exceptions, numerous studies support Ostfeld's (1985, 1990 and references therein) territoriality model. That is, females use territories to defend a resource -- food -- particularly when the resource is patchily distributed. Males also use territories to defend a resource, females. When population density is low and females widely

dispersed, males may adopt a more mobile search strategy as opposed to defending territories. There is also evidence, particularly among Peromyscus, that females may defend territories to protect neonates from infanticide, although results are equivocal (Wolff 1989, Wolff and Cicirello 1989). Numerous studies have demonstrated a reduction in home range area following the provisioning of supplemental food (Boutin 1989). The implication is that food, not density, affects home range size. Following from Ostfeld's (1990) "females in space" model, male wood mice (Apodemus sylvaticus) alter their home range size in response to the availability of reproductively active females.

When viewed from a holistic perspective, the variation in field studies of home range and population fluctuations, the collinearity found by Gaines and Johnson (1981), and the support for alternative models (Ostfeld 1985, 1990), make it unlikely that home range size and spacing alone regulate population size. There may be a threshold or minimum home range size that, when coupled with aggressive interactions (i.e., the Chitty hypothesis) and/or dispersal, may result in intrinsic regulation. Since there appears to be relatively little support for the Chitty hypothesis, future studies should investigate the relationship between both home range size, and if variation in home range size in turn influences emigration rates.

Dispersal

Theory. The social subordinate hypothesis proposed that as population density increases, resource availability declines (Christian 1970). The decrease in resources

would result in increased levels of aggression, in turn forcing socially subordinate individuals to disperse into suboptimal habitats. The saturation-presaturation hypothesis (Lidicker 1975), designed to describe microtine population cycles, recognized two types of dispersers. The first kind, presaturation dispersers, are individuals that disperse prior to relatively high densities. The hypothesis assumes that such individuals would be in relatively good physical condition, yet relatively sensitive to overcrowding. The second kind of individuals are those that disperse during saturated or overcrowded conditions. Saturated dispersers would include old individuals, juveniles, and generally weak and diseased individuals. The social cohesion hypothesis assumes that dispersers are individuals who have had relatively little interaction with their kin (Bekoff 1977). Such asocial individuals are less likely to recognize relatives, whereas more "socially active" individuals could increase their fitness through kin selection and should be less likely to disperse.

One of the more widely recognized dispersal models that is related to population demography is the source-sink model (Pulliam 1988). The model assumes a heterogeneous landscape comprised of two different types of habitats: optimal and suboptimal. The optimal and suboptimal habitats must be within dispersal distance of each other. In optimal habitat reproductive rates are greater than mortality rates; in suboptimal habitat reproductive rates are less than mortality rates. Consequently, the population in the suboptimal habitat is maintained by individuals dispersing from the optimal habitat; thus, dispersal determines densities in the sink population. Conversely, the rate at which individuals disperse from the optimal habitat into the

suboptimal habitat can regulate the density of the source population; that is, the sink can regulate the source population. When surplus in the source habitat equals the deficit in the sink habitat, the two components of the population are in equilibrium. Recently, Watkinson and Sutherland (1995) have shown that sources and sinks cannot be identified by simply comparing measurements of birth and death rates. This was attributed to dispersal depressing fecundity or increasing mortality as a result of density-dependence. They suggested caution when attempting to identify genuine sink population and provide examples to aid in the process.

Gonzalez-Andujar and Perry (1993) used the discrete-time logistic model to examine the effects of dispersal on population dynamics. They assumed $N_{t+1} = A\ N_t\ (1\text{-}N_t)$, where N_t is the population density at time t and A is the per capita growth-rate. Stable equilibria through chaotic behavior were generated by varying A. By steadily increasing the dispersal rate out of a chaotic population (there was no dispersal into the population), the dynamics became oscillatory, then stable, and finally resulted in extinction. Dispersal out of a non-chaotic donor population into a chaotic receiving population resulted in the receiving population exhibiting oscillatory behavior. For two populations, chaos was almost non-existent with two-way dispersal between a donor and receiver population. Results were similar for both density-dependent and density-independent dispersal.

Empirical Evidence. Krebs et al. (1969) coined the term "fence effect" to describe high density vole populations in which a barrier precluded dispersal. The term resulted from a study of enclosed *Microtus* populations in a central Indiana

grassland. One of the enclosed or fenced populations increased to a density about three times greater than a control. The high densities resulted in overgrazing and starvation. Krebs et al. (1969) concluded that dispersal was necessary to regulate and limit vole densities below the carrying capacity (see Ostfeld 1994 for a recent discussion). Subsequently, numerous studies have relied on removal grids and spatiotemporal variation in small mammal demography to study dispersal. Dispersal has been found to be positively correlated with density in populations of M. ochrogaster (Myers and Krebs 1971, Gaines et al. 1979), Townsend's voles (Microtus townsendii; Krebs et al. 1976), and bank voles (Clethrionomys glareolus; Kozakiewicz 1976). In one investigation, Myers and Krebs (1971) found no association between M. pennsylvanicus population density and the number of dispersers on a removal grid. More specifically, Tamarin (1977) found that 39% of the variation in the number of dispersers could be accounted for by density of a control population in the island species M. breweri; 66% of the variation in the number of dispersers onto a removal grid was accounted for by density on a control plot of mainland M. pennsylvanicus. As previously discussed, if intrinsic regulation occurs it is probably the result of several variables acting in concert. Gaines and Johnson (1984) used stepwise multiple regression and principal components analysis in an effort to determine the amount of variation accounted for, and relative importance of, demographic variables in determining dispersal. Results varied depending upon age class and season, although population density was important in explaining the number of dispersers, overall.

However, they concluded that dispersal was density-independent since a constant proportion of the population dispersed at different densities.

Van Horne (1982) studied deer mice (Peromyscus maniculatus) populations in different seral stages of spruce/fir forests in southeastern Alaska. She determined that young of the year, juveniles, did not breed and that over-winter survival was a critical component of fitness -- the majority of individuals died within the first year. Using discriminant function analysis, Van Horne distinguished between adult and juvenile habitats. The adults were dominant over the juveniles and forced them from the optimal habitat. The distinction between optimal and suboptimal was based largely on reduced survival in the suboptimal habitat. During the final year of the study, adult reproduction was of a sufficient level so that juvenile dispersal accounted for higher densities in the suboptimal habitat than in the optimal habitat. Van Horne's work provides support for Pulliam's (1988) model among small mammals. The source population determined the density of the sink population, whereas the sink population regulated the source. Recently, Paradis (1995) tested Pulliam's source-sink model using four populations of Mediterranean pine voles (Microtus duodecimcostatus) in southern France. Two of the populations occurred in what was recognized as high-quality habitat and two in low-quality habitat. Densities were similar between the four populations, regardless of habitat quality. However, the two populations in low-quality habitat had lower recruitment and survival as compared to the high-quality habitat populations. Paradis (1995) concluded that immigration between the high-

quality habitat populations was responsible for the observed variation in density. Furthermore, immigration allowed the population in low-quality habitat to persist.

Extrinsic Interactions

Abiotic

Theory. By the mid-1970s, the density-dependent paradigm of population ecology and of competition-structured communities in community ecology had led to a general perception that natural systems were in some form of stable equilibrium (Peters 1976). This equilibrium perspective was called into question by Wiens (1977). Wiens argued that the main assumption of traditional competition theory (i.e., a resource limited stable equilibrium) was rarely satisfied due to large scale environmental stochastic events. Such stochastic events resulted in "ecological crunches"; these were periods of time when resources were limited, competition for the limited resources strong, and there was intense natural selection for resource utilization traits.

The intermediate disturbance hypothesis relied on this recognition of periodic environmental stochastic events for maintaining coexistence (Connell 1978). Disturbance could shift the competitive advantage between populations of different species. The hypothesis assumed that rapidly occurring disturbances favor good colonizers that would eventually come to dominate the community. Rare or infrequent disturbances would favor populations of competitively superior species, which would

eventually come to dominate the community. Intermediate levels of disturbance, both in frequency and intensity, would provide a "balance" between the life history strategies used by different species, in turn permitting coexistence (Connell 1978).

Huston (1979) used computer simulations to demonstrate how disturbance permitted coexistence. He simulated both two- and six-species systems. In both cases the individual populations had different rates of increase. Disturbance events were modeled so as to result in a density-dependent reduction (50%) in the population size of all species. The disturbances substantially increased coexistence and decreased the time to extinction of all populations.

An alternative life history strategy for coping with environmental stochastic events is what is referred to as the "storage effect" (Warner and Chesson 1985). The storage effect assumes that good recruitment during favorable years is responsible for maintaining the long-term persistence of a population. Recruitment during adverse years is not adequate to offset mortality rates and the population declines. However, some of the individuals produced under favorable conditions are "stored" until the necessary environmental conditions for high recruitment occur again. The storage effect would result in population dynamics with rapid, periodic increases in density, followed by a more gradual decline in numbers.

A more precise, mathematical extension of the storage effect, and one that incorporates coexistence, is the lottery model. The lottery model assumes that short-term environmental instabilities can lead to long-term stability (Chesson and Huntly 1989). The short-term and long-term time scales are united by three concepts. First,

environmental changes covary with competition. As environmental favorability increases for a species, so does its abundance and ultimately competition (i.e., increased competition is an indirect effect of environmental change). Second, there are differential responses among species to environmental fluctuations. Although two species may simultaneously respond positively or negatively to a given environmental change, the magnitudes of the responses must differ. Third, species exhibit subadditive growth rates, which is the result of reduced competition in an unfavorable environment as compared to a favorable environment. Subadditive growth can buffer a population against the joint effects of an unfavorable environment and competition, resulting in low growth rates. The subadditive model can be contrasted with the superadditive model. Jointly favorable conditions can result in superadditive growth rates. Superadditivity occurs in a favorable environment, as compared to the subadditive model, resulting in high growth rates.

Although the previous disturbance hypotheses were intended primarily for community ecology (i.e., how species coexist within a community), they have important implications for population ecology as well. If the rate of a particular environmental stochastic event is substantially increased, the population density of a species favored by disturbance would increase in density and result in the subsequent competitive exclusion (i.e., declining density) of a second species; the opposite is also possible, where a population increases in numbers due to a reduction in the frequency of disturbance events, causing a population decline of a species favored by

disturbance. In addition, the theory clearly illustrates how stochastic events can be responsible for large, density-independent fluctuations in the dynamics of populations.

Empirical Evidence. Unfortunately, there have been few direct tests of the role of disturbance in determining small mammal population dynamics, probably due to the length of time required and difficulties in manipulating environmental stochastic events. The one exception to this is fire. Numerous studies have examined the importance of fire in determining small mammal demography, although most investigators have not attempted to place their work into a broader theoretical context.

The effects of fire on small mammal populations has been examined in grassland (Birney et al. 1976, Bock and Bock 1978, Swanepoel 1981, Rana 1985, Koehring 1986, Gruebele and Steuter 1988, Schramm and Willcutts 1983), savanna (Tester 1965, Beck and Vogl 1972), brushland (Howard et al. 1959, Lawrence 1966, McGee 1982), desert (Ojeda 1989, Simons 1991, Yensen et al. 1992), clear cuts (Tevis 1956, Sims and Buckner 1973, Fala 1975), coniferous forest (Ahlgren 1966, Bock and Bock 1983, Martell 1984), and deciduous forest (Yunger, in review). Responses to fire vary widely among small mammal species and habitats. Working in sacaton grassland in Arizona, Bock and Bock (1978) recorded an increase in hispid pocket mouse (Chaetodipus hispidus), southern grasshopper mouse (Onychomys torridus), and Merriam's kangaroo rat (Dipodomys merriami) numbers after spring fire relative to unburned controls; hispid cotton rats (Sigmodon hispidus) declined in number. In grassland reserves of central Africa, several species of small mammals (primarily an African soft-furred rat [Praomys natalensis] and a striped grass mouse [Lemniscomys

griselda]) showed differential responses to spatiotemporal variation in vegetation and fire (Swanepoel 1981). A similar pattern was observed in a Ugandan grassland (Neal 1970). The differential responses to fire caused changes in abundance, both within the burned site and in adjacent unburned sites. Kaufman et al. (1983) observed a strong increase in P. maniculatus numbers following spring burns in tallgrass prairie. In the same study, R. megalotis exhibited a neutral response, while M. ochrogaster and Elliot's short-tailed shrew (Blarina hylophaga) declined in numbers relative to controls. In prairie, there is generally a negative relationship between the densities of P. maniculatus and litter depth and foliage coverage, which is determined largely by fire (Kaufman et al. 1988. Schramm and Willcutts 1983); M. pennsylvanicus is often absent after prairie fires and the removal of litter (Schramm and Willcutts 1983). Thus, short-term instability (i.e., periodic fire) can contribute to long-term stability (i.e., coexistence of P. maniculatus and M. pennsylvanicus in the same habitat).

In northeast Minnesota, Beuch et al. (1977) found that in a jack pine stand P. maniculatus increased in density due to a greater supply of jack pine seeds immediately following a fire. Martell (1984), working in black spruce forests of northcentral Ontario, found a 2- to 25-fold increase in P. maniculatus numbers as soon as one week after fire. The number of mice remained high for up to a year. Least chipmunks (Eutamias minimus) increased in density following fall fire but not after spring fire. The spruce forest fire resulted in a rapid, long-term reduction in C. gapperi and masked shrew (Sorex cinereus) densities (Martell 1984). In the boreal forest of northern Quebec, Crete et al. (1995) compared four stages of post fire succession (4

yr, 25 yr, 50 yr, and 75 yr post-burn). They also found that P. maniculatus increased in abundance due to disturbance by fire and that C. gapperi was associated with mature forest. They concluded that fire-induced changes in food availability was responsible for determining mammal abundance. In oak forest in southern Michigan, Yunger (in review) found that P. leucopus, like P. maniculatus, increased in numbers following forest fire. Northern short-tailed shrews (Blarina brevicauda) declined in abundance, presumably due to a reduction in litter and duff in which tunnels are constructed.

Although fire is not common in desert systems (McLaughlin and Bowers 1982), two studies have documented the effects of burns on small mammal populations. Simons (1991) compared population dynamics in burned and unburned areas for 13 months both pre- and post-fire. Most of the species (white-throated woodrat [Neotoma albigula], Arizona pocket mouse [Perognathus amplus], and Bailey's pocket mouse [Chaetodipus baileyi]) showed numerical declines following the burn, most notably N. albigula. Simons (1991) concluded that N. albigula declined as a result of fire decreasing food availability and direct mortality as their stick nests burned. An increase in D. merriami abundance was attributed to the fire creating additional open microhabitat. Similarly, following a fire in the Monte Desert of northern Argentina, Ojeda (1989) recorded an increase in the number of saltorial gerbil mice (Eligmodontia typus). Two other species common at the site, the vesper mouse (Calomys musculinus) and gray leaf-eared mouse (Graomys griseoflavus), declined following the fire. However, as pointed out Ojeda (1989), it is unclear whether the decreases are the

result of changes in vegetation due to the burn, a change in predation intensity, or competition with increased numbers of E. typus.

Generally, species of Peromyscus, Dipodomys, Onychomys, and others that feed heavily on seeds and/or exhibit ambulatory or saltatorial locomotion respond positively to fire. Fire commonly increases seed availability (e.g., serotinous cones of the jack pine) and facilitates ease of movement of ambulatory or saltatorial species by reducing ground cover (i.e., foliage and litter). Microtines and shrews, mammals whose distribution is influenced by the presence of leaf litter and foliage in which runways are constructed, usually have a negative response to fire. Interactions between food availability and cover commonly result in a fire-neutral response by Reithrodontomys spp. and some species of Spermophilus. The previous work on fire ecology provides support of Connell's intermediate disturbance hypothesis among small mammals. The populations of some species increase in numbers, while others show a corresponding decrease.

Ice storms may also be responsible for causing rapid declines in small mammal density (Yunger, this study). A severe ice-storm in a northern Illinois tallgrass prairie caused a crash in P. leucopus and M. pennsylvanicus numbers. The effects of the storm were most pronounced on Microtus. Peromyscus populations began increasing the summer following the ice-storm, whereas Microtus populations did not begin to recover until nearly a year and a half after the storm. The effect was also clearly density-independent. Microtus pennsylvanicus densities were two-and-a-half times greater on plots which had the vertebrate predators excluded as compared to controls.

Following the ice-storm, voles were absent on most of the eight plots, regardless of treatment. Sampling initiated following the ice-storm showed the effects were widespread across the landscape and not confined exclusively to prairie; small mammal densities in woodlots, shrubby-oldfields, and non-native grasslands were also extremely low.

Somewhat contrary to the traditional view of populations declining as a result of disturbance, is the work of Meserve et al. (1995). Small mammal densities were estimated over a four-year period in coastal northcentral Chile. The first two years of data were collected prior to an El Niño Southern Oscillation (ENSO). ENSOs, which generally last about one year, occur on average every four years (range: 2-10 y) (Cane 1983). In many areas of coastal Chile, ENSO events result in increased levels of precipitation and in increased seed production (Gutiérrez et al., unpublished manuscript). During the second two years of the investigation, an extended ENSO occurred. For the three regularly occurring species at the site (olivaceous field mouse [Akodon olivaceus], Darwin's leaf-eared mouse [Phyllotis darwini], and degu rat [Octodon degus]), this resulted in a 10- to 30-fold increase in densities within 4 to 8 months. The increased densities were the result of increased recruitment and increased survivorship, probably due to increased plant productivity (Meserve et al. 1995).

One of the few direct tests of the previous disturbance models involved comparisons of recruitment and survival rates between S. hispidus and M. ochrogaster (Doonan, personal communication). The two species competed for similar resources. Under favorable environmental conditions, S. hispidus typically had higher population

growth rates than M. ochrogaster. However, under poor environmental conditions M. ochrogaster had higher survival and population growth rates than S. hispidus. Thus, each species' demography would fluctuate in response to environmental variability, increasing the probability of coexistence. The S. hispidus-M. ochrogaster system provided support for Chesson's lottery model among small mammals. Additional investigations, similar to Doonan's, are needed.

Intraspecific competition

Theory. Relatively simple models, such as the logistic equation, have been used to describe maximum densities resulting from intraspecific competition for a limiting resource. Such competition may also be tightly intertwined with social regulatory factors, such as territoriality, dispersal, and reproductive activity. However, most empirical studies have relied on either naturally occurring spatiotemporal changes in resource availability or experimental manipulation and the subsequent monitoring of demographic responses. That is, how demographic changes occur as a result of variables extrinsic to the population. Consequently, I have included intraspecific competition for limiting resources under extrinsic interactions. It should be recognized, however, that the mechanisms for numerical responses to changes in resource availability may be attributed to changes in territoriality, dispersal, and reproduction that have been reviewed earlier. Consequently, whenever possible, numerical fluctuations in response to resource availability will be related to changes intrinsic to the population.

The now-classic HSS hypothesis (Hairston, Smith, and Slobodkin 1960) proposed that the "world was green" because predators limited herbivores; herbivores in turn had relatively little impact on primary production. Implicit within the model was that herbivores did not deplete their food source and, consequently, would not be food limited; this would include small mammals (although see Hairston 1993). The HSS hypothesis was later refined so that, starting with strong competition in the top trophic level and the exploitation of food resources, alternating trophic levels would in turn compete for and depress their food source (Menge and Sutherland 1976). Also around this time, Schoener (1974) proposed that among vertebrates in general, competition for food would limit population size.

The role of food availability in determining population size has subsequently been refined using ratio-dependent models. Although ratio-dependent models have been applied primarily to predator-prey interactions (see "Predator-Prey" below), there have been attempts to relate them to food-herbivore dynamics as well. Ginzburg and Akçakaya (1992) modeled the relationship between the level of primary productivity and herbivore abundance as: $RP - DP - f\left(\frac{P}{H^{\alpha}}\right)H = 0$, where P represents the plants, H represents the herbivores, R is primary productivity, D is plant mortality rate, f is the rate of consumption of plants by an average herbivore, and α is a measure of the degree of interference among consumers while utilizing resources. The model predicted that an increase in plant productivity will lead to a corresponding per capita increase in herbivores.

Empirical Evidence. Limiting resources, including food, nest sites, microhabitat, and space, have been demonstrated for a wide diversity of taxonomic groups (e.g., Branch 1975, Smith and Cooper 1982, Watkinson 1984, Arcese and Smith 1988, Boutin 1989). With the possible limited exception of nest site availability (Wolff et al. 1985), resource limitation in most small mammals appears to be determined by food availability (Brown et al. 1986, Vessey 1987, Ostfeld 1990). In a review of vertebrate food supplementation studies, Boutin (1989) cited 62 investigations that pertain to small mammals. In general, he concluded that individuals with supplemental food had higher body weights, smaller home range sizes, and advanced breeding when compared to controls. Supplemental food typically resulted in a two- to three-fold increase in density. However, the dynamics of food-supplemented populations did not differ from the dynamics of control populations. Of the 62 small mammal food supplementation studies cited by Boutin (1989), 42 (67.7%) pertain to only three taxonomic groups: sciurids (n=16), microtines (n=15), and sigmodontines (n=11). The latter two, in particular the genera Microtus and Peromyscus, have been well studied and deserve a more detailed inspection.

Several studies have elucidated the importance of food as a limiting factor of microtine populations (Andrzejewski 1975, Bujalska 1975, Gilbert and Krebs 1981, Taitt and Krebs 1983, Taitt et al. 1981, Desy and Batzli 1989, Saitoh 1989, Schweiger and Boutin 1995). Table 1 summarizes the results of ten food supplementation studies with Microtus. Of the eight studies reporting population density, five (62.5%) recorded a significant numerical increase to food augmentation. The investigators

Table 1

Summary of results of Microtus food supplementation experiments

Species	Effects on*: Density	Reproduction	Immig.	Survival	Home range	Weight	Author
M. californicus	+	D+/P+		A0/J0			Ford and Pitelka (1984)
M. californicus					S-/O+		Ostfeld (1986)
M. californicus	0					0	Krebs and DeLong (1965)
M. ochrogaster	0			A+/J+		+	Cole and Batzli (1978)
M. ochrogaster	+	P+		0	0	F0/M+	Desy and Batzli (1989) Desy et al. (1990)
M. pennsylvanicus	+			A+/J+		+	Desy and Thompson (1983)
M. townsendii	0	D+/P0		A0/J0	S-/O	+	Taitt and Krebs (1981)
M. townsendii	+	D+/P+		A+/J	S-/O	+	Taitt and Krebs (1983)

(Continued on following page)

Table 1.-- Continued

M. townsendii	+		A+/J	S-/O	Taitt et al. (1981)
M. townsendii				S-/O	Vickery (1984)

* + indicates an increase, - a decrease, and 0 no change in various parameters. F = female, M = male, A = adult, J = juvenile, D = duration of breeding season, P = proportion of individuals, S = home range size, O = home range overlap. A blank space indicates data not available.

attributed increased densities resulting from supplemental feeding to decreased mortality, increased immigration, increased reproductive success, and decreased home range size. Work with several species of sciurids has resulted in similar findings (Mares et al. 1976, Sullivan and Sullivan 1982, Sullivan et al. 1983, Sullivan 1990, Klenner and Krebs 1991).

Similarly, food supplementation studies with sigmodontines rodents commonly resulted in increased densities. Table 1 summarizes the results of 13 food supplementation studies with Peromyscus. Of the 11 studies reporting population density, nine (69.2%) recorded a significant numerical increase to food augmentation. Four studies distinguished between numerical responses of males and females. In all four cases females increased in density while males did not. Increased female densities have been attributed to different combinations of decreased home range size, and increases in survival, reproductive success, and immigration. Of the 13 studies reviewed in Table 2, all but two were conducted in woodland; the role of food limitation in grassland Peromyscus populations needs further investigation.

Studies of woodland Peromyscus populations provide limited support for Ostfeld's territoriality model. Aggressive territorial defense occurs between females (Rowley and Christian 1976, Whitsett et al. 1979, Ayer and Whitsett 1980). Size of female territories decrease with increasing food availability (Table 1). High to moderately low densities of females result in males defending territories (Table 1 citations). Males may shift territorial boundaries in order to maximize overlap with females (i.e., males exhibit a stronger response to female "resource" availability than

Table 2

Summary of results of Peromyscus food supplementation experiments

	Effects on*:						
Species	Density	Reproduction	Immig.	Survival	Home range	Weight	Author
P. polionotus	F+/M0	+	0		-		Smith (1971)
P. maniculatus	F+/M0	D+/P+		A0/J-		+	Fordham (1971)
P. maniculatus	+	D0/P+	+	0		0	Gilbert and Krebs (1981)
P. maniculatus		D+/P+	+	A0/J-	S-/O	+	Taitt (1981)
P. maniculatus					S0/O		Wolff (1985c)
P. leucopus	+	0		A+/J+	-		Bendell (1959)
P. leucopus	+	D+/P0		A-/J+	S/O+	+	Hansen and Batzli (1978)
P. leucopus	F+/M0	D+/P0	0	+	0	0	Hansen and Batzli (1979)

(Continued on following page)

Table 2.-- Continued

P. leucopus	F+/M0	0	0	0	0		Wolff (1986)
P. leucopus	0	0	0	0	0		Vessey (1987)
P. leucopus	+	D+/P0	+	+		0	Yunger (this study)
P. mexicanus	0	+	0				Dequette and Millar (1995)
P. gossypinus	+		+	-		0	Young and Stout (1986)

* + indicates an increase, - a decrease, and 0 no change in various parameters. F = female, M = male, A = adult, J = juvenile, D = duration of breeding season, P = proportion of individuals, S = home range size, O = home range overlap. A blank space indicates data not available.

food resource availability; Sheppe 1966, Fairbairn 1977, Wolff 1985a). Very low densities of females result in the breakdown of male territorial boundaries (Fairbairn 1978, Nadeau et al. 1981). It should be recognized, however, that there is extensive variability in the work to date and that the previously mentioned conclusions are tentative.

Ostfeld's model predicts the breakdown of female territories when food is abundant; field studies suggest this does not occur (Table 2 citations). A possible explanation is infanticide. Several Peromyscus spp., including P. maniculatus, have promiscuous mating systems (Dewsbury 1981). The promiscuous mating results in uncertain paternity. This suggests that males should rarely commit infanticide. However, laboratory and field studies have shown that females regularly practice infanticide (Ayer and Whitsett 1980, Wolff 1985b, Wolff and Cicirello 1989). This results in aggressive territorial defense between females regardless of food availability. However, even if female defense of territories is independent of food availability, increased availability of food results in smaller territory size.

Due to the relatively short duration of food supplementation, lack of controls and replication, and variation in the type of supplemental food (e.g., rolled oats, sunflower seeds, wheat, corn, and rodent chows are some of the supplemental foods used in the studies listed above) patterns, or the lack thereof, in the response of small mammal populations to food supplementation must be viewed with some caution. Vessey (1987) and Wolff (1989) came to similar conclusions in their reviews of small mammal food supplementation studies and behavior studies. More rigorous experimental

designs and a more detailed reporting of data analyses would aid in future summaries of such experiments, such as the use of meta-analysis (Gurevitch and Hedges 1993). In addition, work needs to be done to see if patterns observed in the Palearctic are the same as in the Nearctic. Finally, previous food supplementation work has not controlled for predators. If predators remove individuals that are the result of supplemental feeding (i.e., a strong predator response to a dense, isolated prey population), it is difficult to detect a treatment response (Cole and Batzli 1978, Ford and Pitelka 1984).

Interspecific competition

Theory. Traditional views of interspecific competition recognized two broad categories, exploitative and interference, which have been defined mathematically by Schoener (1976, 1978). Subsequently, in his review of field experiments on interspecific competition, Schoener (1983b) distinguished between six types of competition: (1) consumptive competition, where an individual consumes a resource, thereby depriving other individuals of that resource; (2) pre-emptive competition, where an individual passively occupies a space so that other individuals are unable to utilize that space (applies primarily to sessile organisms); (3) overgrowth competition, where one or more individuals grow over or upon another individual, thereby depriving that latter individual of some essential resource and/or harming the latter individual by physical contact; (4) chemical competition, where an individual produces a harmful compound (toxin) that diffuses through a media or across a substrate and

damages another individual; (5) territorial competition, where an individual defends either by direct aggression or behavioral signals a unit of space against other individuals; and (6) encounter competition, where interactions between mobile organisms lead to one or more individuals being harmed (e.g., loss of energy, theft of food, injury).

However, Yodzis (1986) argued that "in order to assess properly the role of competition in nature, we need a broader theoretical framework" (p. 480). Accordingly, he suggested three ways in which competition may control community structure: (1) niche controlled, which is based on consumptive competition and community structure resulting from niche differentiation; (2) dominance controlled, which is based on spatial competition with clearly dominant species and community structure resulting from dominance relations; and (3) founder controlled, which is based on spatial competition with no clear functional dominants and community structure resulting from colonization.

Empirical Evidence. Interspecific competition has been best studied within and among North American microtines and sigmodontines. The extensive literature available on *Microtus* and *Peromyscus* food habits indicates a low degree of dietary overlap between the two genera (see reviews by Mumford and Whitaker 1982, Baker 1983, Batzli 1985), suggesting little competition for food. M'Closkey and Fieldwick (1975) found a low to moderate dietary overlap between *P. leucopus* and *M. pennsylvanicus* based on Horn's (1966) index. Consequently, it is likely that there would be at the most limited competition for food.

Although direct competition for food may not be important between microtines and sigmodontines, evidence suggests that Microtus may limit the numbers of other small mammal species through behavioral interactions. In the laboratory, M. pennsylvanicus was clearly dominant over P. maniculatus (J. A. Yunger, personal observation). Encounters between individuals of the two species resulted in a submissive response (usually fleeing) by P. maniculatus. Microtus was also able to monopolize a food source (Purina Rodent Chow) in laboratory enclosures.

Several field studies have relied on spatiotemporal variations in small mammal densities to infer competition. Blaustein (1980) showed that both reproductive success and densities of the R. megalotis and M. musculus were inversely correlated with the presence of M. californicus. Petticrew and Sadleir (1974) found the presence of P. maniculatus to be inversely correlated with densities of the creeping vole (M. oregoni). Wirtz and Pearson (1960) found a similar correlation between P. leucopus and M. pennsylvanicus. These papers suggest that Microtus may be the behaviorally dominant rodent in several temperate small mammal assemblages and negatively influence densities of subordinate species. Linzey (1984) concluded that M. pennsylvanicus excluded or greatly reduced numbers of the southern bog lemming (Synaptomys cooperi) in particular habitats. In this case, the two were in direct competition for food.

Field experiments have shown competition to be an important force structuring ecological communities (Schoener 1983b, but see Connell 1983). Removal experiments resulting in competitive release of small mammals suggest competition

may be important in structuring small mammal assemblages (e.g., Dueser et al. 1989, Holbrook 1979, Brown et al. 1986). However, the results of such studies should be interpreted with caution since experimental investigations of small mammal competition have traditionally been plagued with poor experimental design and other methodological shortcomings (Galindo and Krebs 1986, but see Schoener 1986a). Using three 0.4-ha enclosures, Grant (1969) tested for competition between the woodland C. gapperi and grassland M. pennsylvanicus during a 17-week experiment. M. pennsylvanicus stayed almost exclusively in grassland. As C. gapperi densities increased in the woodland, a greater number of individuals were captured in the grassland. However, the rate at which individuals moved into the grassland was influenced largely by the abundance of Microtus. Three studies have experimentally investigated competition between Peromyscus and Microtus. Redfield et al. (1977) tested for competition between P. maniculatus and M. townsendii in coastal British Columbia. Densities of P. maniculatus increased following removal of M. townsendii on a treatment plot and decreased following reintroduction as compared to a control plot. Using a similar design, Abramsky et al. (1979) obtained similar results working with P. maniculatus and M. ochrogaster in Colorado short-grass prairie. Grant (1971) reported that P. m. gracilis (a woodland subspecies) increased activity in an adjacent grassland as numbers of M. pennsylvanicus were experimentally reduced; high densities of Microtus resulted in competitive exclusion of Peromyscus. None of these studies attempted to determine the type of interspecific competition responsible for the observed changes, although Grant (1971) suggested aggressive interaction, not

resource limitation, may have been responsible. However, the previous experiments provide support for laboratory and field observations that, throughout much of temperate North America, species of Microtus. competitively exclude other small mammal species.

In arid regions of the Southwest United States it is generally accepted that competition is important in determining the number of small mammal species and individuals at a particular location. The limited resource is generally assumed to be seeds, competed for among a guild of granivorous rodents, particularly members of the family Heteromyidae (Brown and Harney 1993). A majority of studies on the granivorous rodent guild have focused on coexistence and community structure, including differential use of different sized seeds through variation in body sizes, microhabitat partitioning (i.e., open vs. covered), and variation in the spatial distribution of seeds (see Brown and Harney 1993). However, two published studies have used removal experiments to quantify the role of interspecific competition in determining population dynamics.

There is a diverse small mammal assemblage in the Chihuahuan Desert of southeast Arizona, including 10 species that were considered to be "not rare" by Brown and Munger (1985). Of the 10 species, seven were classified as granivores. The largest of the granivores, the banner-tailed kangaroo rat (Dipodomys spectabilis), was excluded from two 0.25-ha plots. All three Dipodomys species (D. merriami and Ord's kangaroo rat [D. ordii]) occurring at the site were excluded from two additional plots. D. merriami and D. ordii showed marginal numerical increases to D. spectabilis

removal. However, an increase in D. spectabilis densities following food augmentation resulted in a significant decrease in its two congeners, providing support that the largest Dipodomys can competitively reduce densities of the two smaller Dipodomys species. Removal of all three Dipodomys species resulted in a 2.8- to 4.5-fold increase in the density of the remaining small granivorous rodents. There was no significant effect of Dipodomys removal on the population dynamics of two insectivorous rodents (northern grasshopper mouse [Onychomys leucogaster]; southern grasshopper mouse [Onychomys torridus]) at the site, providing support for the hypothesis that interspecific competition for seeds plays an important role in determining population densities of granivorous small mammals in the desert Southwest United States (Munger and Brown 1981, Brown and Munger 1985, Brown et al. 1986). Similarly, work in the Chihuahuan Desert of New Mexico documented a 2.5-fold increase in desert pocket mouse (Chaetodipus penicillatus) densities following exclusion of Dipodomys spp. (Freeman and Lemen 1983).

In addition to the rodent manipulation carried out by Brown and Munger (1985) and Brown et al. (1986), the experimental design also included ant removal. However, in the absence of all granivorous ant species occurring at the site, rodent densities did not increase. Alternatively, a similar study in the Sonoran Desert of southern Arizona recorded a significant increase in granivorous rodent densities following the removal of granivorous ants (Brown and Davidson 1977). With the exception of the two previous studies, the vast majority of experiments on interspecific competition among small mammals have been confined to the order Rodentia and exclusively to the class

Mammalia. Future work should examine competition among higher taxonomic levels, such as between herbivorous rodents, lagomorphs, and ungulates; granivorous birds, ants, and rodents; and possibly, herbivorous and phloem-feeding insects and small mammals.

Outside of North America there have been several investigations (although a still inadequate number) on interspecific competition among a variety of small mammal taxa. Four field experiments have been carried out in the Neotropics.
August and Fleming (1984) briefly discussed the results from an investigation in the Venezuelan llanos. Competition was tested between a cotton rat (Sigmomys [= Sigmodon] alstoni) and cane mouse (Zygodontomys brevicauda) by removing the latter species from a 1.9-ha plot for 10 months. Although Zygodontomys did not respond numerically to removal of the purported competitor, it was suggested that the results were equivocal due to insufficient data and confounding variables.

In the central Chilean Andes (2,400 m), Simonetti et al. (1985) used three 0.05-ha plots to test for competition between the Andean field mouse (Akodon andinus) and yellow-rumped leaf-eared mouse (Phyllotis xanthopygus). One plot served as an A. andinus removal, the second as a P. xanthopygus removal, and the third as a control. After ten consecutive nights of trapping, the cumulative number of individuals captured in the absences of their purported competitor was greater on the removal plot as compared to the control plot. However, the results are difficult to interpret since the response by Akodon was attributed to individuals "caught in a rock outcrop" and the response by Phyllotis was attributed to individuals "caught in a

shrubby patch" (p. 24). In addition, the relatively small plots (0.05 ha) are only sufficient for testing behavioral-level responses, not population-level increases in densities. In the temperate rainforests (Nothofagus) of southern Chile, reciprocal removal experiments found little evidence for competition between the olivaceous field mouse (Akodon olivaceus) and O. longicaudatus (Murúa et al. 1987). Mid-way through the 21-month experiment, identities of the removal species were reversed on the two 0.5-ha manipulation plots. As compared to a 1.2-ha control, neither of the target species showed a significant numerical response. There was a weak numerical response by the long-haired field mouse (Akodon [=Abrothix] longipilis),

As part of a large-scale experiment on biotic interactions, one of the most intensive studies on small mammal interspecific competition has been conducted in the Mediterranean scrub of northcentral Chile (Meserve et al. 1996). The dominant small mammal in the system, the degu (Octodon degus), was excluded from four 0.56-ha plots for 4 years. Although there was strong evidence for behavioral responses by A. olivaceus to O. degus exclusion (Yunger and Meserve, in review), numerical responses were relatively weak and intermittent. A third species of small mammal that was relatively common in the community, Darwin's leaf-eared mouse (Phyllotis darwini), showed no numerical response to O. degus exclusion. Thus, on the west side of the Andes, competition does not appear to play an important role in structuring small mammal communities. This may be attributed to a relatively low degree of specialization (Meserve 1981a, b, personal communication) and the small mammal species having evolved in relative isolation (Meserve and Glanz 1978, Meserve and

Kelt 1990). Ironically, throughout the rest of the Neotropics, a region that contributed significantly to the competition-structured community paradigm of the 1970s (MacArthur 1972), it is not possible to make even general conclusions on interspecific competition among small mammals.

Laboratory studies have shown that of the two Apodemus species found in Great Britain, the yellow-necked wood mouse (Apodemus flavicollis) is competitively superior to its smaller congener A. sylvaticus (Hoffmeyer 1973, Montgomery 1978). This led Montgomery (1981) to carry out reciprocal removal experiments in which A. flavicollis was removed on one plot, A. sylvaticus on a second plot, and a third plot used as a control. In the absence of their congener, both species entered reproductive condition earlier than on the control. This led to increased densities of A. flavicollis but not A. sylvaticus. There appeared to be marginal competitive release in space use, leading Montgomery (1981) to conclude that interspecific competition was relatively weak due to intrinsic differences of the two Apodemus species. In the Namib Desert of southern Africa, Hughes et al. (1994) studied competition between the nocturnal dune hairy-footed gerbil (Gerbillurus tytonis) and diurnal four-striped grass mouse (Rhabdomys pumilio). Rhabdomys was excluded from the study site, an isolated "island" of vegetation located between two sand dunes. Sand tracking showed an overall increase in Gerbillurus activity following Rhabdomys removal despite temporal differences of activity.

Even with the experimental design limitations of many small mammal studies, the previous work clearly demonstrates that interspecific competition can play a role in

determining small mammal population dynamics. What needs to be recognized is that the strength of the interactions can vary widely. For example, in Chile, competition may play only a minor role in determining small mammal population dynamics; in temperate areas of North American, interspecific competition can result in competitive exclusion and the absence of a species within a habitat. Future questions on competition among small mammals need to address what is the timing and magnitude of the interaction.

Predator-Prey

Theory. Discrete predator-prey interactions can be modeled using difference equations which assume non-overlapping generations. In his monograph on arthropod predator-prey interactions, Hassell (1978) describes numerous variations of the discrete predator-prey equations. The models are widely applicable not only to arthropods but also to vertebrates and potentially small mammals. Alternatively, classical continuous-time predator-prey models assume continuous reproduction (Holling 1959, Rosenzweig and MacArthur 1963). Predators encounter prey at random, and the trophic function depends on prey abundance only. Such models may have limited applicability to homogeneous systems in which population dynamics operate on a rapid scale; their validity in most natural systems, however, has been questioned (Arditi et al. 1991). Arditi and Ginzburg (1989) have proposed that instead of the consumption rate being determined by a function of prey abundance only ($g = g(N)$; i.e., prey dependent), the rate should be expressed as a function of prey

abundance per capita ($g = g(N/P)$; i.e., the prey to predator ratio). Where g is the trophic function, N is prey abundance, and P is predator abundance (for a complete mathematical treatment see Arditi and Ginzburg 1989). The dynamic properties of the two models differ significantly. Prey-dependent models predict that an increase in productivity will result in an increase in only predators, not prey, and that predators vary in response to prey abundance, not vice versa. Ratio-dependent models predict that predator and prey abundance will covary (i.e., both can increase simultaneously) and that "the level of prey equilibrium does react to predator removal" (Arditi and Ginzburg 1989, p. 322). It should be recognized, however, that not all students of predator-prey models support the ratio-dependent approach. It has been argued that ratio-dependent predation models which make very specific assumptions and have relatively little generality for consumer-resource theory (Gleeson 1994) should only be used when the predator and prey are the top two trophic levels in an ecosystem (Sarnelle 1994), and do not have a mechanistic basis. Patterns and experiments cited in support of the ratio-dependent model may also support alternative approaches (Abrams 1994)

Erlinge et al. (1984, 1988) have developed a model based on the type III functional response that incorporates prey switching by generalist predators. The model assumes a relatively diverse generalist predator guild with alternative prey species and/or alternative habitats. Erlinge and his colleagues predicted that predators will damp-out fluctuations in small mammal populations dynamics. In other words, a small mammal population rapidly increasing in density will be "cropped" by predation.

The type III functional response suggests that prey populations will experience reduced rates of predation while at low densities. An alternative approach has been developed by Sinclair (1989) and Sinclair et al. (1990). Sinclair and his colleagues predict that at low densities small mammal population dynamics are predator regulated. Predators are not able to respond to rapid increases in prey densities due to different rates of intrinsic increase between the predators and the prey (i.e., a predator time-lag). Consequently at high densities, prey populations become limited by resources, not predators.

Empirical Evidence. Experiments have shown that predators play an important role in limiting, for example, aquatic insect (Peckarsky 1985, Gilliam et al. 1989), snail (Osenberg 1988), zooplankton (Kerfoot and DeMott 1980, DeMott and Kerfoot 1982), terrestrial insect (Huffaker et al. 1984, Riechert and Bishop 1990), and spider (Spiller and Schoener 1988) populations (see also Sih et al. 1985). The extent to which terrestrial vertebrate populations, including small mammals, are controlled by predation has been a controversial topic (Erlinge et al. 1984, Henttonen et al. 1987, Kidd and Lewis, 1987, Erlinge et al. 1988, Hansson and Henttonen 1988).

Correlations between terrestrial vertebrate prey and predation intensity have often been used to infer predator regulation of prey populations. For example, Steen et al. (1990) provide evidence that suggests a predator eradication program in Norway during the early 1900's was responsible for increased numbers of small game species and the reduction of cyclicity in vole populations. Using straw to increase cover, Taitt et al. (1981) recorded significantly higher survival rates of M. townsendii as compared

to control plots. They concluded that the straw reduced the rate of predation, and in turn, increased survival. Goszczynski (1977), Southern and Lowe (1982), and Erlinge et al. (1983) provide observational evidence that prey switching by generalist predators may dampen or eliminate rodent and shrew population cycles. Fitzgerald (1977), Henttonen (1985), Henttonen et al. (1987), and Keith (1990) have shown correlations between increased predator abundance and the onset of cyclic declines and population lows in microtine rodents. The implication is that predation is at least partially responsible for causing and maintaining the declines. Using published trap records and model fitting, Akçakaya (1992) showed that the snowshoe hare (L. americanus)-lynx (Lynx canadensis) 10-year cycle can be predicted using a ratio-dependent predator model when coupled with food availability.

Population field studies that manipulate the predators of terrestrial vertebrates are limited. By reducing the number of red fox (Vulpes vulpes) and marten (Martes martes) on an island off the coast of northern Sweden, Marcstrom et al. (1988, 1989) observed a numeric increase in both tetraonids and arctic hares (Lepus timidus) as compared to a reference island. Following large-scale shooting of fox (Vulpes vulpes) and feral cats (Felis catus) in New South Wales, Australia, Newsome et al. (1989) concluded that predation influences rabbit populations (Oryctolagus cuniculus). Specifically, predators regulated low densities of prey; high prey densities resulting from an increased food supply (the result of heavy rains) were not regulated by predators (Pech et al. 1992). Their investigation provides support for Sinclair's (1989, Sinclair et al. 1990) predator specialist model.

A limited number of field experiments have excluded vertebrate predators and compared demographic responses on the exclusion plots to controls. Taitt and Krebs (1983), working in southwest British Columbia, used fish nets to "stop predation by the Great Blue Heron" p. 839. They reported a significant increase in both survival and densities of M. townsendii. The investigators did not, however, replicate the treatment or control for terrestrial predators. Working with M. agrestis in a southern Swedish grassland, Erlinge et al. (1990) excluded avian and terrestrial predators on one 0.5-ha plot. Survivorship was significantly greater on the predator exclusion plot as compared to a control plot, the increased survivorship resulting in increased densities. Reid et al. (1995) excluded avian and terrestrial predators from an 11 ha plot in the Northwest Territories for three years. During the course of their study, and for three years prior to their predation study (Krebs et al. 1995), collared lemming (Dicrostonyx kilangmiutak) densities were extremely low (0-2 individuals per ha) (Reid et al. 1995). The investigators concluded that the densities were low because "predation mortality is sufficient and necessary to limit summer population growth in these microtine species." p. 387. However, a reanalysis of their data shows that the slopes, for both years in which there was sufficient data to calculate the slopes, are nearly identical between the predator exclusion plot and the three controls. A constraint of the previous investigations is that the manipulations were not replicated and/or sampling was carried out only intermittently or for relatively short durations.

Desy and Batzli (1989) and Desy et al. (1990) studied artificially seeded populations of prairie voles (M. ochrogaster) in a central Illinois bluegrass field using

an impermeable design with dispersal sinks. Using replicated 0.13-ha plots they detected a significant increase in vole densities and survival at the end of 24 weeks on predator excluded plots; food supplemented plots showed a significant increase in density. Meserve et al. (1996) excluded vertebrate predators from eight 0.56-ha plots for four years. Small mammal demography was monitored using standard mark-and-recapture techniques. As compared to controls, predator exclusion clearly had an effect on prey densities and survivorship. The magnitude of the effect varied widely both between species and temporally within a species. Following from dietary analysis of the predators, species that experienced the greatest predation intensity showed the greatest numerical response to the manipulations: O. degus had strong numerical increases, P. darwini had moderate intermittent numerical responses, and A. olivaceus showed relatively little response. All three species showed a significant increase in survivorship in the absence of predators. Yunger (this study) investigated the effects of vertebrate predators on M. pennsylvanicus, P. leucopus, and P. maniculatus demography. Both avian and terrestrial predators were excluded on four 0.6-ha plots in northern Illinois tallgrass prairie for three years. The experiment showed that following an annual peak in densities and the cessation of reproduction, predators significantly reduced Microtus densities. The increase in density on the exclusion plots was attributed to a significant increase in survivorship. Predators had no significant effect on Peromyscus densities. The differential effects of vertebrate predators on small mammal demography may be attributed to preferential selection of Microtus vs.

Peromyscus, as reflected in the predators' diet (Randa 1996, Cooper, unpublished data).

Hanski et al. (1993) provided a particularly interesting test of the classical continuous-time predator-prey model cited above. They tested the model using data on Microtus (prey) and Mustela (predator) interactions. For both the predator and prey equations, a term describing a type II functional response was included. Presumably, they used a type II functional response because the data came from Fennoscandia, a region that is typified by comparatively low prey diversity and relatively little habitat heterogeneity. Prey switching and a type III functional response is unlikely to occur in such systems. Since the mustelids only breed following a critical threshold in prey density, the model also incorporated a term in the predator equation where predator growth rate was a function of the predator-prey ratio. Below the threshold the predators did not breed; above the threshold predators compete for prey. A similar term was included in the prey equation. The prey only breed throughout the winter (defined as 6 months) if fall densities are below a particular threshold. This pattern of reproduction was documented in the field using extensive live-trapping. The dynamics generated by the model closely fit observed time series of Microtus and Mustela population dynamics in Fennoscandia. Using a nonlinear analysis, both the model and empirical dynamics showed chaotic behavior along with a statistically significant periodic component. The authors concluded that delayed density dependence imposed by Mustela led to the chaotic dynamics.

The Interaction of Interactions

Theory. In recent years the importance of multiple biotic interactions has been widely recognized (Hunter and Price 1992, Matson and Hunter 1992, Power 1992, Strong 1992). Although the concept of "bottom-up" vs. "top-down" forces is not new (Hairston et al. 1960, Menge and Sutherland 1976), the recognition that both can be important in determining the dynamics of populations and the structure of communities is relatively recent (Leibold 1989, Matson and Hunter 1992, Power 1992, Strong 1992). Such forces have been well studied with invertebrates and in aquatic systems (Hunter and Price 1992, Power 1992), yet virtually ignored among terrestrial vertebrates (see Desy and Batzli 1989, Krebs et al. 1995 for exceptions). There are several reasons to suspect that a multifactorial experiment on top-down vs. bottom-up effects could help to elucidate mechanisms controlling small mammal demography (e.g., complex population dynamics observed at mid-latitudes, work with other taxonomic groups, work in aquatic systems, the single factor food supplementation experiments discussed above). However, there is still continued debate as to whether multifactor approaches are useful for the study of small mammal population dynamics (Gaines et al. 1991, Lidicker 1991, Lidicker 1994). In order to address questions such as why food supplementation studies commonly result in only a two-fold increase in densities, and how predator switching behavior may regulate prey populations, simultaneous manipulation of food from the bottom-up and predators from the top-down is required.

Recently, Stenseth (1995) used the approach of fitting a time series model to long-term data on population dynamics. He shows that the number of dimensions embedded in the model should reflect the number of interactions responsible for generating the observed time series. Using population data from a time series of L. americanus, three time-lags (i.e., dimensions) best describe the dynamics. Thus, in theory, a three trophic-level interaction should be responsible for determining L. americanus density.

A second type of interaction between interactions that can occur includes competition and predation. Holt's (1977) apparent competition model is based on two competing prey species and a predator. The predator has a negative effect on both prey species while both prey have a positive effect on the predator. Thus, an increase in predator abundance by consuming prey species one will also have an adverse effect on prey species two. This leads to prey species one indirectly having a negative impact on prey species two mediated through the predator. However, the negative interaction between the prey is not due to resource limitation, hence the term apparent competition.

Empirical. Three field experiments have examined the interaction between top-down and bottom-up effects on small mammal populations dynamics (Desy and Batzli 1989, Krebs et al. 1995, Yunger this study). (A fourth top-down vs. bottom-up experiment [Taitt and Krebs 1983] was not replicated and did not include an interaction [i.e., both food supplemented and predator excluded]; consequently, it will be discussed only under empirical studies of predation and food availability.) In

addition to investigating predation and food availability independently, Desy and Batzli (1989) experimentally examined how the interaction of the two interactions regulate terrestrial vertebrate populations. The results of the interaction indicate additive and equal effects on density. That is, both biotic interactions were significant and of relatively equal importance. Food supplementation and predator exclusion also resulted in a significant interaction for body growth rates and adult body size. The significant interaction was attributed to predators inhibiting the growth response to supplemental food, as a result of more restricted movements.

In an effort to determine what causes the L. americanus cycle, Krebs et al. (1995) carried out one of the largest-scale field experiments ever undertaken. Working in the Yukon, mammalian predators were excluded from two 1 km^2 areas using electric fencing. Supplemental food (rabbit chow) was spread ad lib across one of the two enclosures and a third 1 km^2 area to which predators had access. The experiment was effective as of January 1989. The food supplementation resulted in 1.5- to 6-fold increases in densities as compare to a control. The numerical response to predator exclusion was similar (1.4- to 6-fold). When averaged over the duration of the study, the food supplementation + predator exclusion treatment resulted in an 11-fold increase in density. During the late decline phase, L. americanus densities were 36 times greater on the interaction plot as compared with the control! The numerical responses of L. americanus to food and predation individually, and, in particular, the food + predator exclosure treatment, provide solid experimental support of the model predicting tri-level trophic interaction determine the population dynamics. In

particular, the food + predator exclosure treatment indicates the biotic interactions interact multiplicatively.

The third top-down vs. bottom-up experiment with small mammals was carried out with P. leucopus in a northern Illinois tallgrass prairie restoration. As discussed previously, work at the same site had shown that food played an important role in limiting P. leucopus numbers during the non-breeding season, while the effects of predation were negligible. However, the top-down vs. bottom-up experiment showed a significant predator x food interaction. Densities were lowest on the unsupplemented - predator access plots, intermediate on the supplemented and unsupplemented exclusion plots, and highest on the supplemented - predator access plots. The significant interaction may be attributed to predators rapidly removing individuals and new ones immigrating onto the plots. The conclusion is supported by increased canid activity around the food supplemented - predator access plots and significantly lower survivorship on the predator access - food supplemented plot vs. the predator access unsupplemented plot.

The investigation by Meserve et al. (1996), previously discussed under competition and predation, is the only experiment with small mammals to have tested for an interaction between the interactions. However, there was no significant interaction between predator exclusion and competitor exclusion for the three species investigated (Ak. olivaceus, Phyllotis darwini, Ab. longipilis). Holt (1977) cites the lagomorph-lynx (Felis lynx) system of Nova Scotia as support for his apparent competition model. Arctic hares (Lepus arcticus) occur naturally on the island.

Following the introduction of L. americanus, L. arcticus noticeably declined in numbers. However, following closer inspection, the two species of Lepus utilized different habitats. Holt concluded that the increased prey biomass contributed by L. americanus resulted in increased F. lynx densities. The increase in predator abundance in turn resulted in a decrease in L. arcticus densities; the two species were not competing for a limited resource.

Large Spatial Scales

Introduction

The study of large spatial scales includes landscape ecology and metapopulation dynamics. Although the importance of spatial scale has long been acknowledged in ecology (McIntosh 1985), it is primarily during the past decade that it has received notable attention. It should be recognized that the two approaches -- landscapes and metapopulations -- are closely interrelated; both are based on heterogeneous or patchy environments. However, the two approaches have been developed largely independently in the literature, each having its own unique set of definitions and terminology (e.g., Hanski and Gilpin 1991a, Turner 1989). In addition, the study of large spatial scales does not necessarily preclude topics reviewed in the previous sections. Predation, competition, and dispersal can all be important determinants of population dynamics, both within and between patches. In fact, it is the inclusion of such factors that forms an integral part of landscape ecology and metapopulation

dynamics, both of which have been shown to have important theoretical and empirical implications for small mammal population dynamics.

Metapopulations

Theory. The term metapopulation was coined by Levins (1970). Motivation to develop the concept came from trying to explain single species population dynamics in a spatially and temporally varying environment. Throughout the 1970s, the primary emphasis in metapopulation investigations was the maintenance of altruistic genes and group selection (Gilpin 1970, Boorman and Levitt 1973, Wilson 1975, 1980). This subsequently led to single species metapopulation models (Hanski 1991). An integral part of these models is a feedback between the proportion of occupied patches and the likelihood of a population going extinct within a patch. Conceptually, this is similar to the "rescue effect" (Brown and Kodric-Brown 1977), where immigration decreased the probability of extinction. Levins' original model assumed that the probability of colonization (ip) was a metapopulation process; the probability of extinction (e) within patches, however, was assumed to be independent of other patches. This leads to the equation $^{dp}/_{dt} = ip(1 - p) - ep$, were p is the proportion of patches occupied by a species. Hanski (1982) modified Levins' model to included the rescue effect: $^{dp}/_{dt} = ip(1 - p) - ep(1 - p)$, making extinction also a metapopulation process.

Subsequently, numerous variations of single-species metapopulation models have been explored (see Hanski 1991, Gotelli and Kelley 1993). For example, multiple stable equilibria can occur when immigration affects population growth rates (Hanski

1985). The immigration of individuals from outside a dynamic system, sometimes referred to as "propagule rain," can result in a mainland-island model (Gotelli 1991). Gotelli (1993) developed a "general" metapopulation model: ${}^{dp}/_{dt} = (a + bp)(1 - p) - (c - dp)(p) = f(p)$. The term $(a + bp)$, which replaces ip in the previous model, is equivalent to the function $g(p) = a + bp$. $g(p)$ assumes the probability of local extinction is a linear function of p, the fraction of sites occupied. Similarly, the term $c - dp$, assumes that the probability of local extinction is also a linear function: $h(p) = c - dp$. In the first term, a and b represent parameters for immigration, a being the contribution of external propagules to colonization, and b is the strength of metapopulation influence on colonization. In the second term, c and d represent parameters for extinction, c is the intrinsic propensity for extinction of a site and d is the reduction in the probability of local extinction caused by adding another site. Recently, Hanski (1994a, 1994b) has developed a series of models which predict patch occupancy using Diamond's (1975) incidence-function approach. The models are based on a first-order Markov chain with two states, the presence or absence of a species within a patch. Subsequent extensions of the models include a mainland-island incidence-function and a metapopulation without a mainland. An important addition to the model is the incorporation of a spatially explicit metapopulation. a, x, and y are three parameters estimating patch area and isolation that can be estimated by nonlinear regression using the patch occupancy data. Hanski (1994a) assumed that $S_i = \sum p_j e^{-\alpha d_{ij}} A_j$, where p_j is 1 for occupied patches and 0 for empty patches, d_{ij} is the distance between patches i and j, and α is a constant setting the distance-dependent migration

rate. Extinction and colonization probabilities E_i and C_j, were defined as $E_i = e/.^0$, where A_i is the area of patch i and $C_j = S^2_i/(S^2_i + y^2)$.

An extension of the single species metapopulation models is what Hanski and Gilpin (1991a) termed metacommunities, when two or more species co-occur in the same patch. These models can produce probability distribution functions for the joint occurrence of two or more species within a patch (Taylor 1991). Numerous other multispecies metapopulation models have been developed that incorporate interspecific competition and predator-prey interactions (see Hanski and Gilpin 1991b). Nee and May (1992) modeled the coexistence of two species in a fragmented landscape. The first species was always competitively superior to the second species and would exclude it from any patch it colonized. The second species was a superior colonizer, allowing it to persist in the system. An interesting outcome of the model is that destruction of habitat fragments resulted in increased abundance of the competitively inferior species.

Empirical Evidence. In a review on patch occupancy models, Hanski (1994b) presents data on colonization and extinction probabilities for three species of shrews from 17 islands (common shrew [Sorex araneus], masked shrew [Sorex caecutiens], and lesser shrew [Sorex minutus]). He uses the data to show how predictions from a metapopulation model without a mainland (Hanski 1994a) can be tested. Hanski concludes that the model can make quantitative predictions about patch occupancy. He goes on to describe how the approach may be applied to conservation biology and management of fragmented landscapes. Lima et al. (in review) monitored four

subpopulations of small mammals in semiarid northcentral Chile for four years. Among five species, extinction rates were determined largely by population size. Colonization rates were most affected by population size and variability, although this applied only to equatorial facing slopes. Most species within their assemblage had higher extinction than colonization rates, leading the investigators to conclude that persistence of the metapopulation for all five species was the result of repeated colonization events.

Although several studies have examined dispersal and, for example, small mammal movement between woodlots (Wegner and Merriam 1979), few have placed them in a metapopulation context. The brevity of this portion of the review illustrates the paucity of studies on small mammal metapopulation dynamics. Small mammal ecologists have only begun to explore the role metapopulations may play in determining population fluctuations both with and across patches. Such models are receiving greater attention in conservation biology (Harrison 1996) and may prove useful for making management decisions.

Landscape Ecology

Theory. Landscape ecology is a discipline that has evolved its own unique set of terminology. Turner (1989) provides an informative review of these terms and how they are related to the quantification of landscape patterns and structure. Briefly, landscape physiognomy refers to the distribution of physical components within the landscape, such as patch isolation. A physiognomically explicit model would

recognize the position of each patch within the landscape. Landscape composition is the relative amount of different habitat types within a landscape. Using different indices incorporating landscape physiognomy and landscape composition, it is possible to quantify landscape structure. Dunning et al. (1992) expand upon Turner's (1989) review in an effort to develop a conceptual framework for the study of population dynamics within complex landscapes. They emphasize four different ecological processes that require a knowledge of the structure of a landscape. Landscape supplementation and landscape complementation are processes that involve the movement of individuals between patches and distinguish between suitable and nonsuitable resources, respectively. The third process is referred to as the neighborhood effect. The neighborhood effect assumes that a species within a patch is influenced more by contiguous patches than by more distant patches within the landscape. Dunning et al.'s (1992) fourth process, source-sink dynamics, has been previously described (see "Dispersal") since it was originally developed as a dispersal model (Lidicker 1975), independent of subsequent landscape concepts; empirical tests have proceeded along a similar line. A potential limitation of the previous approach would be logistical constraints imposed by attempts to quantify and monitor numerous patches across a relatively large spatial scale.

Bondrup-Nielson and Ims (1987) developed a population dynamic model that varied habitat heterogeneity, dispersal, and territoriality. Their model assumed that females would establish territories to defend quality patches of habitat. Dispersal was modeled as a function of distance between patches and within-patch density. Their

model predicted that high levels of habitat heterogeneity would lead to stable population dynamics; fluctuating or cyclic populations would occur in more homogenous landscapes. It is interesting that the predictions of the previous model are the same as the model developed by Erlinge et al. (1983, 1988; see "Predation"). Yet the predicted dynamics are the result of mechanisms.

Empirical Evidence. Similar to metapopulation dynamics, there have been few spatially explicit tests of how variation among several (i.e., ≥3) habitat types or patch complexities influences small mammal demography. A notable exception was a study by Bondrup-Nielsen (1987). He used populations of C. gapperi in northern Alberta to test Bondrup-Nielson and Ims' (1987) model. The site was a heterogeneous mix of trembling aspen (Populus tremuloides), white spruce (Picea glauca), black spruce (Picea mariana), and bogs. Litter size remained relatively constant throughout the study and was independent of habitat type. However, density, persistence, recruitment, and home range size varied considerably between patches. He concluded that unlike other Clethrionomys spp. that have cyclic populations, C. gapperi has relatively stable population dynamics. C. gapperi differed from the cyclic species in that space was generally available for the establishment of territories. However, the space may be in poor-quality habitat. Bondrup-Nielson went on to suggest that the relatively stable population dynamics of C. gapperi observed at the site may be attributed to habitat heterogeneity, providing support for the model.

The majority of studies addressing questions on habitat heterogeneity have limited their scope to two habitat types (e.g., Van Horne's 1982 and Paradis' 1995

source-sink investigations). Although these studies have been useful and informative, the addition of variation among several habitat patches would help to further elucidate the relationship between population dynamics within a patch and global dynamics. Future work may require a team approach, such as the cooperation of several investigators collecting data on habitat structure, behavior, demographic dynamics, and competitors and predators located within the habitat matrix.

Conclusions and Future Directions

It has been over 75 years since Elton (1924) published his seminal review of potential causes of mammalian population cycles. During this time there has been extensive research in the area of small mammal demography, particularly during the past 25-30 years. If the goal of small mammal population ecology is to quantitatively predict what causes long-term changes in density, then the goal has not yet been reached. However, I would suggest that a more modest goal of qualitative short-term (ca. 3-4 years) predictions either has been, or is close to, being attained.

This review should clearly illustrate that two or more factors may be responsible for determining small mammal populations at any given time. Consequently, a greater emphasis will have to be placed on multifactorial approaches if more quantitative predictions of population dynamics are to be achieved. The few studies conducted along these lines suggest the interaction of interactions may be important. For example, home range size and overlap, territorial defense, and dispersal may all play a role in determining population dynamics. However, to simply say that population

density is regulated by dispersal, without examining how density starts to increase or decrease as home range size changes in response to fluctuating resources, is inadequate. For some of the better studied taxa, it is clear that food availability is important in limiting densities. This pattern needs addition confirmation outside of North America, particularly in the Southern Hemisphere. Food availability may also be tightly linked with some of the previous intrinsic population parameters. Larger, more complex field experiments will be required to tease apart the timing and magnitude of these different variables. With some notable exceptions, interspecific competition appears to occur widely among small mammal species. This results in lower numbers of the inferior competitor. Also, densities of the inferior competitor can fluctuate in response to numerical changes of the superior competitor. The role of predation appears to be more variable. Depending on the taxa and environment of interest, predators may or may not play an important role in determining small mammal population dynamics; additional field experiments are still needed.

In the past 75 years there have been extensive theoretical developments in population ecology, with a wealth of empirical studies on small mammals. As has been repeatedly echoed in ecology, theorists and empiricists need greater interaction. In no other field of population ecology is this more evident than in studies on small mammals. The majority of studies reviewed above, particularly those on extrinsic factors, did not set out to test a model. As has been emphasized by McIntosh (1985) and Krebs (1988), theorists need to consult with field biologists in an effort to build tractable, testable models; empiricists need to pay greater attention to basic

mathematics in order to design rigorous experiments to test models. With some important exceptions, I would suggest that the two parties still operate too independently. This is of particular importance in the light of current conservation issues. We simply cannot study all species in all systems. If ecology is to contribute significantly to conservation biology, a minimal level of predictability will have to be obtained.

CHAPTER 2

FIELD SITE AND EXPERIMENTAL DESIGN

Study Site

The study site is located at Fermi National Accelerator Laboratory (Fermilab) in northern Illinois. The lab is a heterogeneous landscape of woodlots, wetlands, agricultural fields, restored prairie, shrubby-oldfields, nonnative grasslands, and developed sites totaling 3,200 ha in area (Illinois Natural History Survey 1985). The experimental manipulation is located in a 32-ha prairie restoration. Prior to 1989 the site was a cornfield; in the spring of 1989 it was plowed, disked, and a mix of prairie grasses and forbs evenly distributed across the site. Thus, the management history of the site provided an ideal setting for large-scale experimental manipulations: a relatively homogeneous environment. Plant coverage at the site is dominated primarily by big bluestem (Andropogon gerardii) and tall goldenrod (Solidago altissima). Precipitation, recorded at a station on Fermilab and approximately 1.5 km from the site, averages 92.5 cm (±2.78SE) annually.

Experimental Design

During the late summer/early fall of 1992 eight 0.6-ha (78 x 78 m) plots were established at the site (Fig. 1). Plots were spaced a minimum of 80 m apart to increase

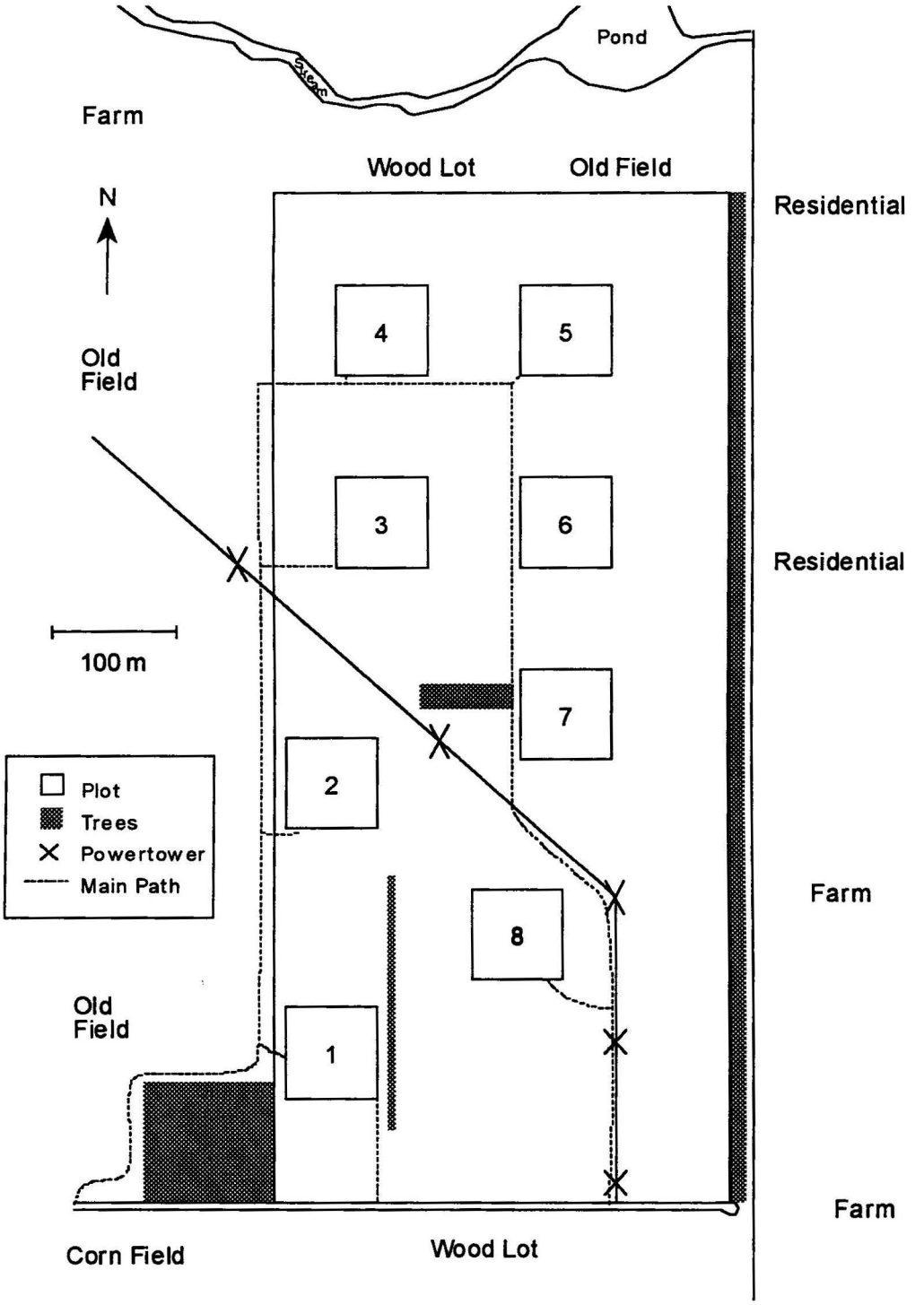

Figure 1. Map of the experimental field site at Fermilab, Batavia, IL, showing the position of the eight small mammal plots.

independence. Each plot has a small mammal trapping grid with a 6 x 6 array of trap stations (n = 36) with 12-m spacing. One 7.5 x 9 x 23-cm Sherman live trap, baited with rolled oats and peanut butter, was placed at each station. Polyester fiber was place in the traps to provide bedding to help reduce stress and provide insulation during winter months. Preliminary trapping was conducted for three consecutive nights on each grid during October and November of 1992. Trapping was reinitiated in March of 1993 and has continued uninterrupted at monthly intervals. Captured individuals were identified to species, marked with a uniquely numbered ear tag, and data taken on date of capture, plot, grid location, mass, sex, sexual condition (males: abdominal or scrotal; females: perforate or imperforate) and reproductive condition (females only: pregnant, dilated pubic symphysis, lactating). Any ectoparasites and/or injuries were also recorded. Peromyscus spp. were aged using pelage characteristic (Conventry 1937, Gottschang 1956, Layne 1968). Microtus were aged using three different criteria, possession of any one of which signified adulthood: (1) duration on the plots (≥3 months), (2) reproductive state (scrotal testes in males and perforate, lactating, or pregnant in females), and (3) mass (males > 28.0 grams and females >26.0 grams). If any one of the three criteria was satisfied, the individuals were classified as an adult (Nadeau 1985, McCravy and Rose 1992). The use of mass for estimating age is controversial (Dueser et al. 1981, 1984, Tamarin 1984) and may not be an accurate classificatory criterion. However, the goal of the investigation was not to describe natural history patterns over time, but to compare controls and treatments. That is, a precise determination of age is not necessary for comparing age structure on the

controls vs. treatment plots as long as aging criteria were the same for both.

In the spring of 1993 construction of terrestrial vertebrate predator exclosures was initiated on plots 2, 4, 6, and 8 (Fig. 1), and was completed by July 1994. The exclosures were constructed using 2-m high, 2.5-cm mesh poultry netting. The top 0.5 m of fencing was angled outward at 45° and had a 0.25-m overhang to prevent predators from climbing over. At ground level, the fencing projected outward for 0.5 m and was staked down to prevent predators from digging under. To date, the fencing has been effective for all but the smallest vertebrate predators (discussed below). During the late summer, fall, and winter of 1993 terrestrial vertebrate predator scats were collected in order to assess dietary preference of the excluded populations.

Low fencing (0.25-m high), over which the predators were readily able to pass, was constructed around the control grids to test for a fence effect on the small mammals (Krebs et al. 1969, Ostfeld 1994). Trap lines inside the plots were periodically compared to two control lines on the north and south end of each control plot. An equal trap effort both in and out of the control plots found the chickenwire had no observable effect on small mammal species composition or numbers. Visual signs, such as direct observations of individual movements, microtine tunnels, and tracks in the snow, provided further support for this conclusion.

In March of 1994 raptor exclusion was effective. Raptors were excluded using 12.5 x 12.5-cm mesh nylon netting suspended above the plots. PVC and bamboo were placed on the control plots to duplicate the perches for passerines on the exclusion plots that resulted from the posts used to support the netting. While excluding

raptors, the 12.5 x 12.5-cm mesh permitted most passerines to pass in and out freely (personal observation).

In March of 1994 sampling was initiated at six alternative prey sites (Fig. 2) in order to quantify species composition and abundance of vertebrate prey throughout Fermilab (Randa 1996, Cooper, unpublished data). Small mammal abundance was estimated by mark-recapture along three, 200-m transects in each of the six locations (Fig. 2). A 7.5 x 9 x 23-cm Sherman live trap, baited with rolled oats and peanut butter, was placed at 12-m intervals along each transect (total of 51 traps per location). Trapping was conducted for two consecutive nights at monthly intervals. Sciurids (gray squirrel [Sciurus carolinensis], fox squirrel [Sciurus niger], woodchuck [Marmota monax], eastern chipmunk [Tamias striatus]), and Ring-necked Pheasant (Phasianus colchicus) numbers were estimated using diurnal visual counts. The abundance of eastern cottontails (Sylvilagus floridanus) was estimated using spot lights during nocturnal counts. The 200-m trapping transects were also used for the visual counts (Randa 1996, Cooper, unpublished data).

The relative abundance of vertebrate predators at the experimental site has been estimated using a variety of techniques. This included direct observation, calls, snow and mud tracking, and the presence of pellets and scat. Starting in March of 1993, systematic monitoring of vertebrate predator activity was begun at the experimental site and each of the six alternative prey locations. Raptor activity was monitored using visual counts and play-back calls (Cooper 1996). Twenty-four scent stations (thirty at

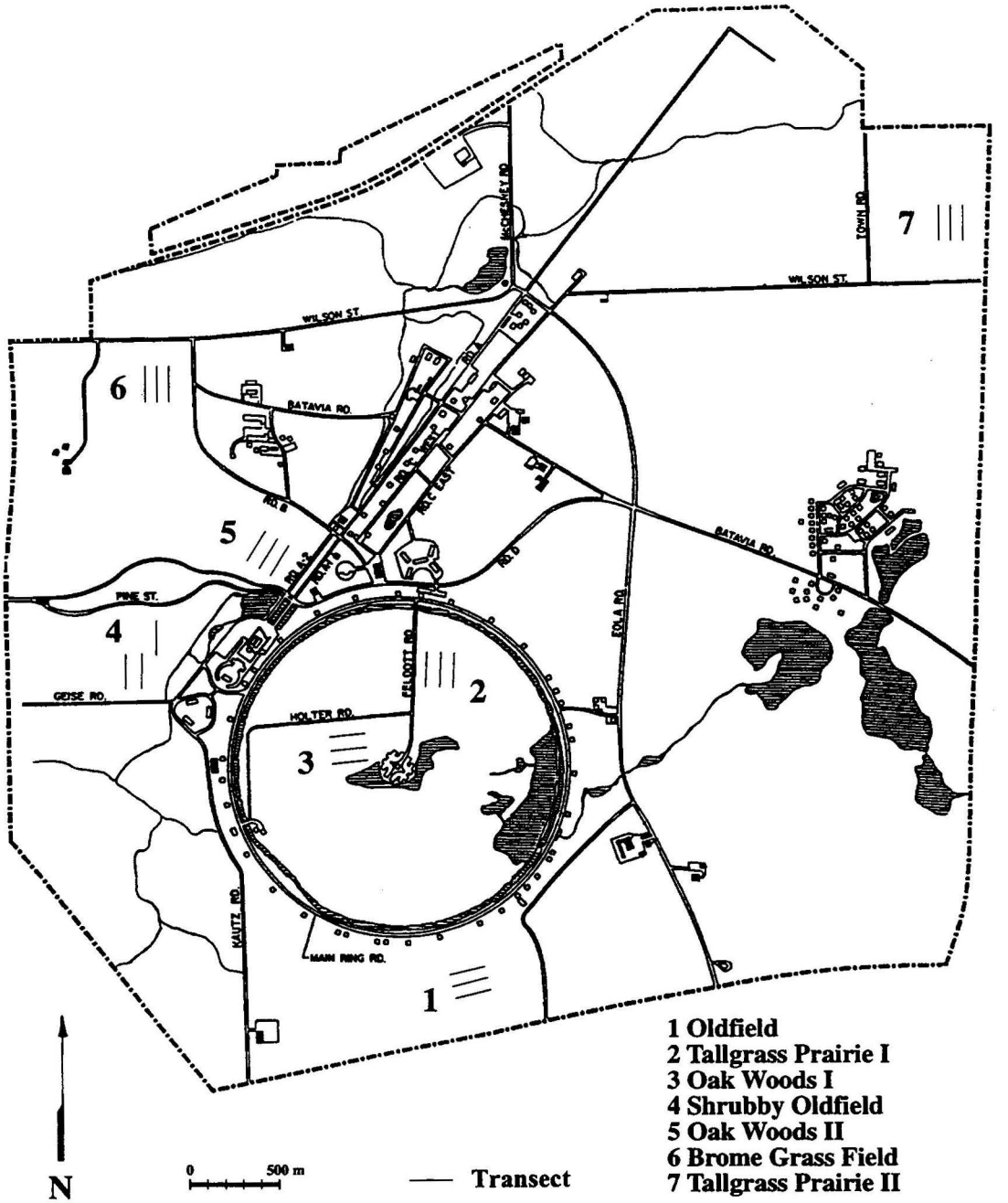

Figure 2. Map showing the location of the experimental site and six alternative prey locations at Fermilab.

the experimental site), arranged in three transects, were lured (using Cronk's Predator 500, Cronk's Trapping Supply, Wiscasset, Maine), on average, for a minimum of two nights twice a month to monitor carnivore activity at the experimental and alternative prey sites (Randa 1996). Tracks were scored from zero (no activity) to three (high activity). Using the previous protocol, tracks were recorded at scent stations placed at the four corners of plots 1, 3, 5, and 7, from February through May of 1995. At the experimental site, snake abundance was estimated using 1.2-m long, 5-cm wide PVC piping, and two sheets of plywood hinged together with numerous 5 x 5 cm boards placed between the two sheets. The PVC and wood shelters were located at 15 stations distributed throughout the site. The stations were checked 2-3 times per month. Captured individuals are marked by scute clipping. In February of 1995 intensive trapping was used to estimate weasel abundance at Fermilab. A total of 100, 7.5 x 9 x 23-cm Sherman live traps, baited with chicken entrails and lured with Cronk's Weasel Lure, were checked daily for three days, then switched to alternative locations for an additional three days. Traps were not placed in a standardized fashion as careful selection of trap placement is necessary when trapping weasels (King 1973, King and Edgar 1977).

The collection of canid scat was expanded to cover all of Fermilab in March of 1994, using standardized routes, and continued until August of 1995 (Randa 1996); raptor pellets were collected by searching for roosts between March 1994 and August 1995 (Cooper, unpublished manuscript).

A food supplementation experiment was initiated in October of 1994, immediately following the monthly small mammal census. Eleven kg of rodent chow (Rodent Breeder Chow, PMI Feeds, Saint Louis, MO) was broadcast by hand on plots 1, 2, 3, and 4 (Fig. 3) per week until the May 1995 small mammal census. Work with a previously established laboratory colony showed that the chow readily supports both growth and reproduction of Peromyscus leucopus, the species of interest in this portion of the field experiment. To examine the effects of a naturally occurring food supply, acorn density was estimated in two of the alternative prey sites, both oak woodlots. The first woodlot (Woodlot I) was approximately 7 ha in area and dominated by bur oaks (Quercus macrocarpa); the second woodlot (Woodlot II) was approximately 10 ha in area and dominated by black oaks (Quercus velutina). Individual acorns were collected and weighed to determine mean mass and multiplied by the mean number of caps + acorns/caps counted in 51, 1-m^2 quadrats to estimate mast biomass per woodlot.

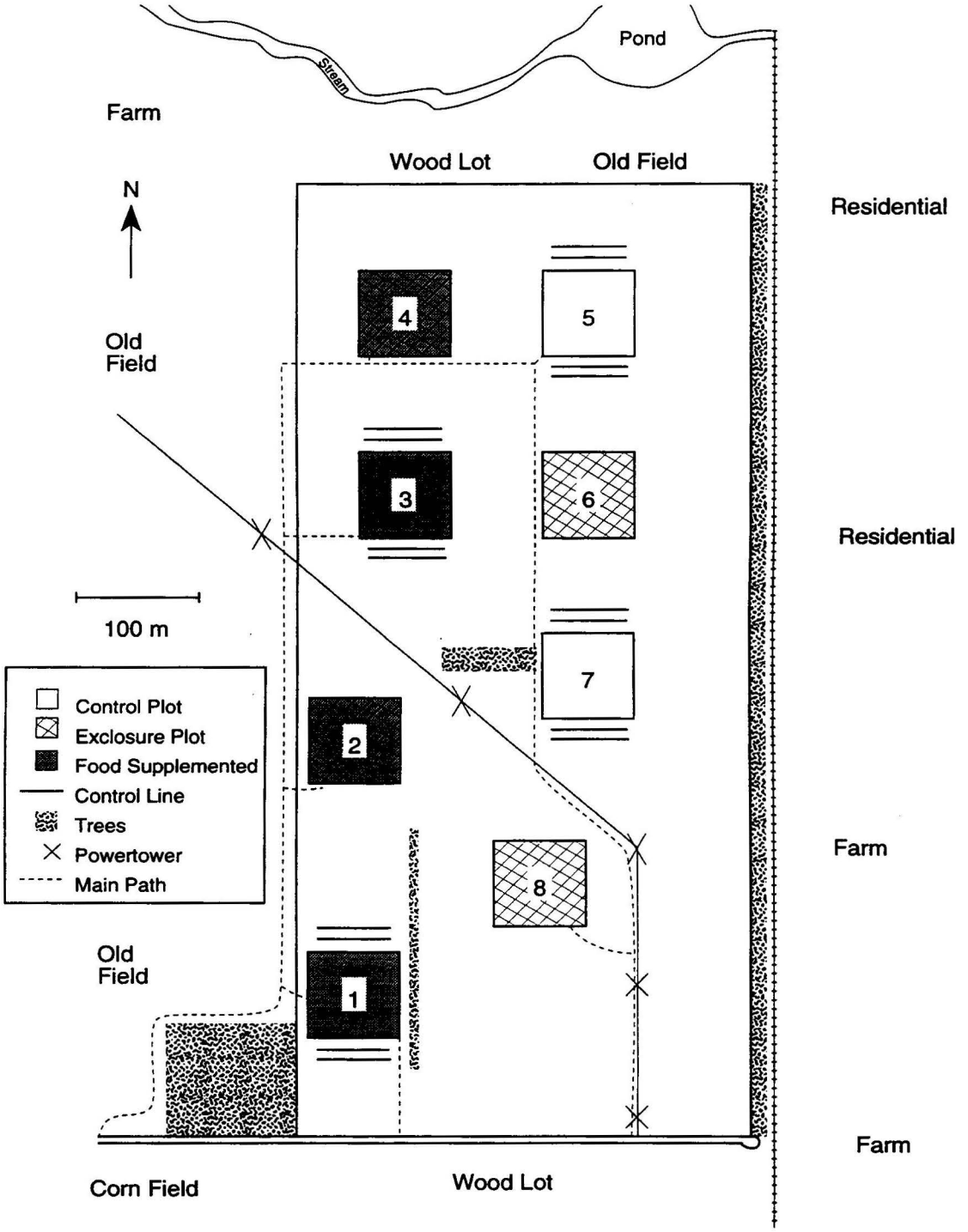

Figure 3. Map of experimental site at Fermilab showing control lines, predator exclusion plots, and from October 1994 to May 1995 food supplementation plots.

CHAPTER 3

DEMOGRAPHIC RESPONSES OF SMALL MAMMALS FOLLOWING VERTEBRATE PREDATOR EXCLUSION: A LARGE-SCALE FIELD EXPERIMENT

Introduction

It is clear that predation plays a role in controlling the populations dynamics of several, if not most, taxa, including populations of aquatic insects (Peckarsky 1985, Gilliam et al. 1989), snails (Osenberg 1988), zooplankton (Kerfoot and DeMott 1980, DeMott and Kerfoot 1982), terrestrial insects (Huffaker et al. 1984, Riechert and Bishop 1990), and spiders (Spiller and Schoener 1988; see also Sih et al. 1985). What is often unclear is the timing and magnitude of the interactions, particularly in regards to vertebrate predator-prey systems (Pearson 1985, Brown and Harney 1993). During the 1980s a vigorous debate developed focusing on the question: can vertebrate predators regulate their prey? (Erlinge et al. 1984, Kidd and Lewis 1987, Erlinge et al. 1988). The past half century has resulted in a wealth of descriptive and observational studies on vertebrate predator-prey systems (e.g., Pearson 1964, 1966, Craighead and Craighead 1956, Fitzgerald 1977, Henttonen 1985, Henttonen et al. 1987, Keith 1990, Steen et al. 1990, Akçakaya 1992). This work has aided in formulating clearly defined hypotheses and developing general predictive models that can be tested in the

field. Investigations have, however, met with only limited success in formulating general conclusions on the role of vertebrates in determining prey populations. Clear conclusions, solid support for models, and the resulting continued debate may be partially attributed to a lack of rigorous field experiments (Pearson 1985, Krebs 1988). For example, even nonlinear correlations which include time-lags do not necessarily imply cause and effect. The effects of changes in plant productivity on prey population dynamics can be distinguished from correlated fluctuations in predator-prey dynamics. In addition, it is still not possible to quantify the magnitude of the predator effect.

There have been a very limited number of experiments on the effects of vertebrate predators on their prey's demography. Avian and terrestrial predators were excluded for three years from an 11-ha plot in the Northwest Territories (Reid et al. 1995). Collared lemming (Dicrostonyx kilangmiutak) densities were extremely low (0-2 individuals per ha) both during the experiment and for three years prior to the predation study (Krebs et al. 1995). Reid et al. (1995) concluded that the lemming densities were very low because "predation mortality is sufficient and necessary to limit summer population growth in these microtine species" (p. 387). However, a reanalysis of their data shows no difference in slopes on the predator exclusion versus to the three controls (for both years in which there was sufficient data to calculate the slopes). A constraint of the previous investigation is that the manipulation was not replicated (although it should be recognized it was a large plot, useful for studying low population densities) and sampling could only be carried out for three months during

the summer. Desy and Batzli (1989) studied seeded populations of prairie voles (Microtus ochrogaster) in a central Illinois bluegrass field using an impermeable design with dispersal sinks. Using replicated 0.13-ha plots, they detected a significant increase in vole densities and survival at the end of 24 weeks on predator excluded plots; food supplemented plots showed a significant increase in density. The results of the interaction indicated additive and equal effects on density. Food supplementation and predator exclusion resulted in a significant interaction for body growth rates and adult body size. Meserve et al. (1996) excluded vertebrate predators from four 0.56-ha plots in semi-arid northcentral Chile for more than four years. The predator exclusion resulted in increased densities of the two largest, numerically common species at the site, Darwin's leaf-eared mouse (Phyllotis darwini) and the degu rat (Octodon degus). However, numerical responses varied between seasons and intrinsic population highs and lows. Predator exclusion resulted in a substantial increase in survivorship for several of the six small mammal species at the site.

I began by focusing on two alternative models. The first, developed by Erlinge and colleagues (Erlinge et al. 1984, 1988), will be referred to as the generalist predator model. The second, developed by Sinclair and colleagues (Sinclair 1989, Sinclair et al. 1990) will be referred to as the specialist predator model. The generalist predator model assumes a relatively heterogeneous landscape. Such a landscape can support different prey species and/or varying densities of the same species in different habitats. Switching between alternative prey provides the necessary food base for the generalist predators to maintain relatively high numbers. Consequently, by maintaining relatively

high numbers, and switching between abundant prey populations, predators are able to depress moderately high densities of prey.

Alternatively, the specialist predator model assumes a relatively homogeneous landscape in which predators feed primarily on a limited number of prey species (i.e., there is not readily available alternative prey to switch to). In turn, a crash in prey numbers will be followed by a sharp decline in predator abundance. Since vertebrate prey nearly always have intrinsic rates of increase that are greater than their predators, the prey can increase numerically at a rate faster than the predators can respond (Jaksic et al. 1992). Consequently, vertebrate predators should have little numerical effect on prey that have increased recently to moderate or high densities. Predators should have a numerical effect on prey after a time lag (one or more years for many vertebrate predators [e.g., Keith 1990]) or when prey numbers are relatively low (e.g., Newsome et al. 1989).

A prerequisite for testing the two previous models is a knowledge of the foraging behavior of the predators at the landscape scale. Specifically, do the vertebrate predators (1) feed on a limited number of species or (2) switch between alternative prey species and/or populations? In regards to this investigation, two lines of evidence provide support for alternative (2). First, since the study was being conducted in a heterogeneous landscape, alternative species and/or habitats were available for switching to occur. Second, information on the natural history of the common predators occurring at the site (see Results) shows that they may be found in a variety of habitats and feed on diverse prey. Consequently, I assumed that Erlinge et al's.

(1984, 1988) generalist predator model should be applicable. Support for the model would follow from results in which densities of a species or population that is experiencing relatively high predation rates would not decline due to exclusion of vertebrate predators.

Data on trap records collected between March 1993 and February 1994 (a period of moderate to high small mammal densities) and August 1995 and February 1996 (a period of low to moderate densities) were used to test the following hypothesis: vertebrate predator exclusion will result in a numerical effect on prey when prey densities are at or near their peak. Several potential mechanisms could contribute to a numerical response of the prey as a result of predator exclusion. Accordingly, I tested the following four potential mechanisms for prey responding numerically to predator exclusion:

(1) a reduction in direct mortality due to predation results in increased survivorship;

(2) increased recruitment due to the decreased probability of estrous females being depredated;

(3) an increase in the proportion of reproductively active females; and

(4) a reduction in predation risk reduces foraging constraints and ultimately increases the procurement of food.

(A fifth potential mechanism, changes in spatial patterns, will be discussed in Chapter 4).

The evidence for increased survivorship is obvious. When an individual is predated, it is removed from the population and its life span decreased. Among

terrestrial vertebrates, one consequence of increased survivorship -- a change in age structure -- has not been previously linked with predation intensity (Chapter 1). As survivorship increases, the age structure of the population should be shifted more towards adults. Thus, a correlate to mechanism (1) is that a reduction in predation intensity may result in a greater proportion of adults in the population.

The evidence for mechanism (2) through (4) is less clear. Under laboratory conditions, Cushing (1986) found that female mice in estrous were more susceptible to predation by weasels. He concluded that weasels used scent omitted by estrous females as olfactory cues for locating individuals. Under reduced predation intensity this should lead to a greater proportion of females. Since one male can inseminate multiple females, and pregnancy and nursing among females limits in situ recruitment, a female-biased sex ratio could result in increased recruitment and density (mechanism (2)). An alternative mechanism through which the reproductive potential of a population (and ultimately density) could be increased following predator exclusion is through an increase in the proportion of reproductively active females (mechanism (3)). Laboratory experiments have demonstrated that the presence of weasels, or the presence of weasel urine, can inhibit reproduction in bank voles (Clethrionomys glareolus) (Ylönen 1989, Ylönen et al. 1992). Support for mechanism three would follow from an increased proportion of reproductively active females due to predator exclusion. However, the extremely high densities of predators under laboratory conditions, and the close proximity of predators and prey, do not adequately represent field conditions (Korpimäki et al. 1994), situations under which experiments with

terrestrial vertebrates are lacking (Magnhagen 1991, Korpimäki et al. 1994). Results of the one field experiment on the effects of predators on reproduction of terrestrial vertebrate prey are equivocal: a reduction in the number of weasels significantly increased the proportion of reproductively active C. glareolus, but not Microtus agrestis (Korpimäki et al. 1994).

Among mammals, weight has been shown to be positively correlated with reproductive success (Eisenberg 1981). In addition, the absence of predators reduces constraints placed on time spent foraging within a patch (Kotler 1984, Brown 1988, Brown et al. 1988, 1992), patch selection (Brown 1988, Brown et al. 1988, 1992, Longland and Price 1991), and routes traversed (i.e., Lagos et al. 1995). Consequently, an increase in weight as a result of predator exclusion can serve as a measure of reduced stress and increased reproductive potential. Neither the sex ratio hypothesis nor weight hypothesis have been tested for terrestrial vertebrate prey species (Chapter 1).

Trap records from the six alternative prey sites were used to determine differential prey availability across the landscape and how vertebrate predator activity responded to differences in prey abundance. Data from the scats and pellets provided information on switching behavior by the predators and if the predators preferentially selected particular species in relation to their regional abundance (i.e., not just abundance at the experimental site; Randa 1996, Cooper, unpublished data).

Data Analysis

Small mammal demographic characteristics (i.e., density, survivorship, reproduction, weight, sex ratios, and age structure) for each monthly census were summarized using the Capture-Mark-Recapture programs of Le Boulengé (1987). Trappability was calculated using Manly-Parr estimates (Seder 1982). Densities were determined using minimum number known alive (MINK) since the number of marked individuals recaptured (*Ri*) commonly did not meet the assumptions of probability estimation techniques (Seder 1982, Pollock et al. 1990). If an individual was captured >1 time within a monthly census, mean body weight per plot was calculated based on only the first capture; pregnant females and juveniles were also excluded from analyses of body weight. Males were defined as reproductively active if testis were descended; female were considered reproductively active if they were perforate, lactating, pregnant, or had a dilated pubic symphysis. To facilitate comparisons of small mammal abundance across the landscape, data from the experimental site were standardized to equal the trap effort of the 200-m transects used for sampling alternative prey abundance. Regression lines were fit to the continuous response variables from the four treatments and F-values calculated to see if higher order polynomials added significant explanatory strength to the models. The best-fit models were then tested for autocorrelation using the Durbin-Watson statistic (Ostrom 1990) produced by SAS PROCEDURE REG (1990a). Since the time series were relatively short, significant autocorrelation was not a problem and treatment effects were tested with an analysis of covariance (ANCOVA) using SAS PROCEDURE GLM (SAS

1990a). ANCOVA is useful for testing for an interaction or homogeneity of slopes (Littell et al. 1991). This provides a particularly sensitive analysis for testing temporal change by crossing the categorical variable (in this case, the presence or absence of predators) with the continuous covariate (in this case, time). Traditional model building techniques were used (Box et al. 1978). Non-significant interactions were removed from the model to increase the sensitivity of lower level interactions and/or main effects. If no significant sources of variation were detected the full model was reported. In some cases both significant interactions (i.e., heterogeneity of slopes) and main effects were present. In such cases caution must be used when interpreting main effects; particularly careful inspection of the graphed and plotted data are advisable. As part of the model building approach, I tested for quadratic responses. This was accomplished by squaring the covariate (i.e., $Time^2$). A significant F-value for $Time^2$ indicated that the data fits a quadratic response; the sign of the parameter estimate of the quadratic term indicating a parabola or hyperbola.

The residuals were inspected for departures from normality using box-plots and normal probability plots (Tukey 1977). All inferences are based on type III sums-of-squares. The May, June, and July premanipulation months were analyzed with MANOVAs using SAS PROCEDURE GLM (SAS 1990a) to test for pre-existing differences. A liberal α level of 0.10 was used for all pretreatment comparisons; all other analyses were considered significant at $\alpha = 0.05$. The data are presented graphically for all significant values appearing in the ANOVA tables and those that are close to significant and/or have ecologically meaningful trends.

Survival analyses were conducted using the log-rank test of SAS PROCEDURE LIFETEST (SAS 1990a). PROCEDURE LIFETEST takes into account right censured observations (i.e., individuals whose fate is unknown when the experiment is terminated; there is no way to determine how long an individual survives after the last trap session). Statistical comparisons of overall survival were conducted with the nonparametric log-rank test, which is robust to differences in survival curve shape and does not assume any particular underlying distribution (Lee 1980, Fox 1993). The ranks were based on the survival distribution functions, calculated as the probability of an individual at time t having a lifetime exceeding t. Multiple comparisons were performed for species with an overall significant survival effect. Since no specific a posteriori tests are available for comparison of multiple survival curves, single probability z-scores were calculated using the covariance matrix generated by PROCEDURE LIFETEST. P-values were then calculated based on the z-scores and significance determined from Bonferonni adjusted α's (Fox 1993).

Results

A diverse and abundant assemblage of terrestrial vertebrate predators was documented at the field site (Table 3), including activity on the control plots and adjacent to the exclosures. Of these, coyotes (Canis latrans) and red fox (Vulpes vulpes) are considered generalist predators, feeding on a wide range of food (Andelt et al. 1987, Van Vuren and Thompson 1982). The remaining species, primarily the least weasel (Mustela nivalis) and long-tailed weasel (Mustela frenata), are more

Table 3

Vertebrate Predators and their relative abundance at Fermi National Accelerator Laboratory

Species	Abundance
Carnivora:	
Coyote (Canis latrans)	High
Red Fox (Vulpes vulpes)	Low-Moderate
Gray Fox (Urocyon cinereoargentius)	Very Low
Least Weasel (Mustela nivalis)	Low-High
Long-tailed Weasel (Mustela frenata)	Low-High
Domestic Cat (Felis catus)	Low
Falconiformes:	
Red-tailed Hawk (Buteo jamacensis)	High
Rough-legged Hawk (Buteo lagopus)	Moderate (Winter only)
Northern Harrier (Circus cyanus)	Moderate (migration and winter)

(Continued on following page)

Table 3 -- (Continued)

American Kestrel (Falco sparverius)	High
Strigiformes:	
Great Horned Owl (Bubo virginianus)	High
Long-eared Owl (Otus otus)	High (primarily winter)
Short-eared Owl (Otus flammeus)	Low (migration and winter)
Eastern Screech-Owl (Asio flamulus)	Low
Squamata:	
Fox Snake (Elaphe vulpina)	Low

specialized, feeding heavily on small mammals (e.g., Sylvilagus floridanus and smaller), and, to a lesser extent, the young of ground nesting birds (King 1990). On two occasions, M. frenata was observed climbing the fencing, suggesting they were not able to pass through the chickenwire. M. nivalis can and did pass through the chickenwire. The six individuals captured on exclusion plots during the course of the study were removed (no M. frenata were ever captured on the exclusion plots). In

addition to the canids, Red-tailed Hawks (Buteo jamacensis) and Great-horned Owls (Bubo virginianus) are common, generalist avian vertebrate predators (Bent 1937, 1938) that occurred at the site. The canids and raptors previously discussed utilize a variety of habitats, including, in particularly at Fermilab: open fields, grasslands, shrubby areas, and edge habitats (Howell et al. 1978, Peterson 1979, Randa 1996, Yunger personal observation).

The results of the raptor and canid foraging are described in detail by Cooper (unpublished manuscript) and Randa (1996). Briefly, Cooper concluded that Microtus was the numerically most important prey of B. virginianus. Sylvilagus occurred in the second greatest proportion of prey consumed, but accounted for the greatest amount of prey biomass. Peromyscus was the third most common prey item, although it accounted for a much smaller proportion of the raptor diets than the previous two prey. The owls also showed a tendency to switch to avian prey during the spring. Randa (1996) concluded that Microtus, Sylvilagus, and Peromyscus were the three most numerically common prey, respectively, of canids as well. When Microtus densities were relatively high, voles and rabbits accounted for the nearly 90% of the prey items, although the latter species accounted for the greatest proportion of prey biomass consumed. During periods of very low Microtus density, the proportion of Peromyscus in the diets increased significantly. Again, Peromyscus still accounted for a substantially smaller proportion of canid diets than either rabbits or voles.

From March 1993 through February 1994 a total of 10 prey species were represented in 7,192 captures of 2,495 individuals (Table 4). Only Microtus

Table 4

Number of individuals captured per species

Species	No. Individuals	Total No. Captures
White-footed Mouse (Peromyscus leucopus)	1184	3788
Meadow Vole (Microtus pennsylvanicus)	777	2331
Deer Mouse (Peromyscus maniculatus)	310	806
Northern Short-tailed Shrew (Blarina brevicauda)	119	132
Masked Shrew (Sorex cinereus)	40	40
Eastern Chipmunk (Tamias striatus)	34	55
Thirteen-lined Ground Squirrel (Spermophilus tridecemlineatus)	11	12
Prairie Vole (Microtus ochrogaster)	9	17
House Mouse (Mus musculus)	6	6
Eastern Cottontail (Sylvilagus floridanus)	5	5
Total	2495	7192

pennsylvanicus, Peromyscus leucopus, and P. maniculatus had adequate sample sizes for subsequent demographic and statistical analyses. These three species accounted for 91% of the individuals and 96% of the captures at the site. Accordingly, analyses were limited only to Microtus and the two species of Peromyscus (primarily P. leucopus). Of the remaining seven species, only Blarina brevicauda was captured in moderate numbers; the remaining species can be considered transitory or not entering the trappable population. Since B. brevicauda has been implicated as a potential small mammal predator (Eadie 1948, 1952, Lomolino 1984), individuals captured on exclosure plots were removed.

Densities of small mammals fluctuated widely during the course of the investigation (Fig 4). Most notable was a dramatic decrease in density between the January and February 1994 censuses. The decline was the result of a severe ice storm. Ice of up to 2 cm thick was recorded on tree branches and effectively coated all of the ground and vegetation in the prairie. The impact of the storm was not isolated to the 32 ha experimental site, but occurred across an area of at least several thousand hectares. Sampling at the six alternative prey sites (albeit only after the storm) revealed very low densities throughout Fermilab as a whole (Fig. 5). Observations at two of the alternative prey sites prior to the storm helped substantiate the effect of the disturbance; while delineating transects during November and December 1993, Microtus abundance was sufficiently high in the shrubby-oldfield and brome grass field so that individuals were observed scattering underfoot. Of the three most important

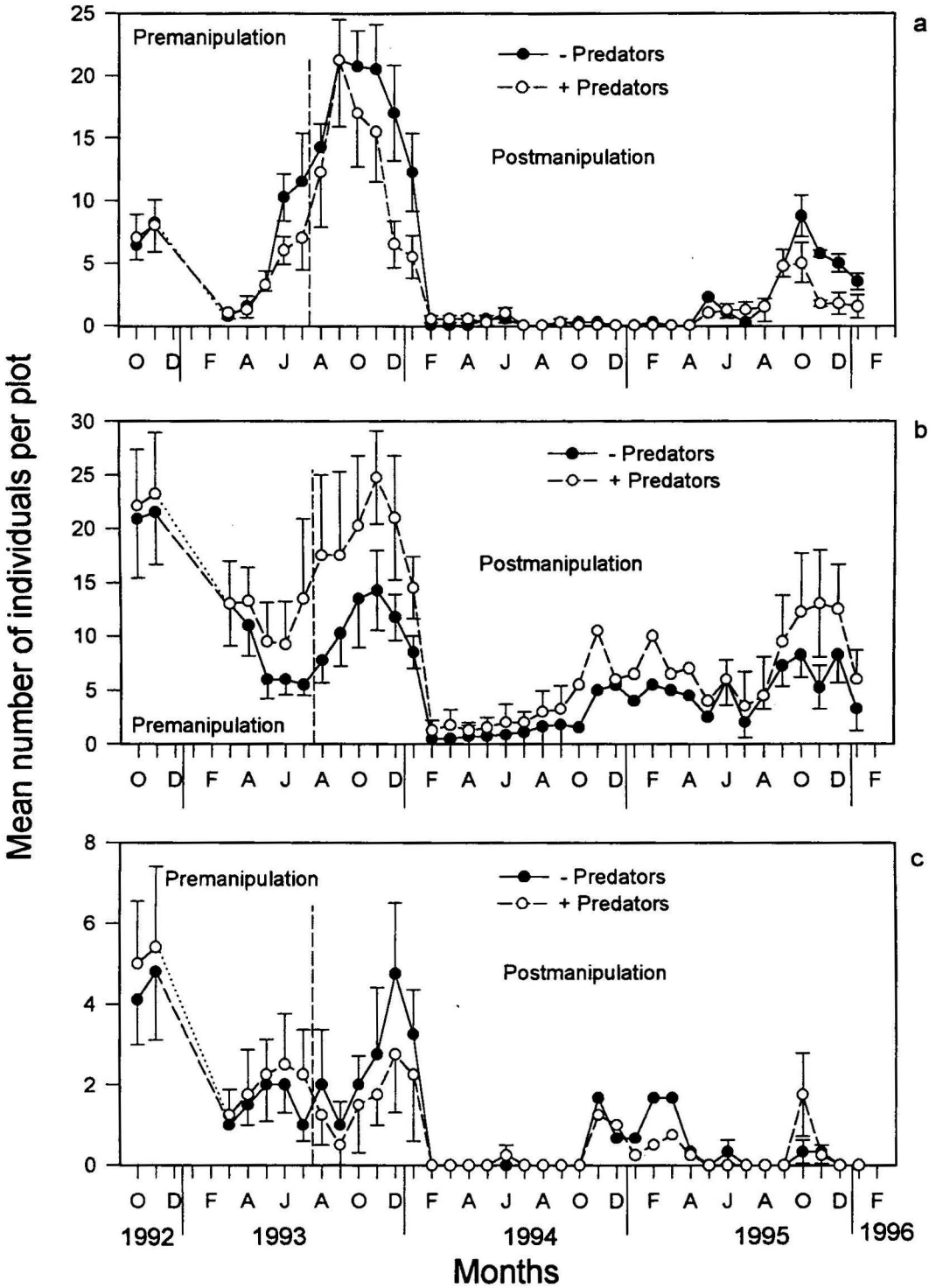

Figure 4. Population dynamics of the three most common small mammal species on the predator access and predator exclusion plots. (a) Microtus pennsylvanicus, (b) Peromyscus leucopus, (c) Peromyscus maniculatus.

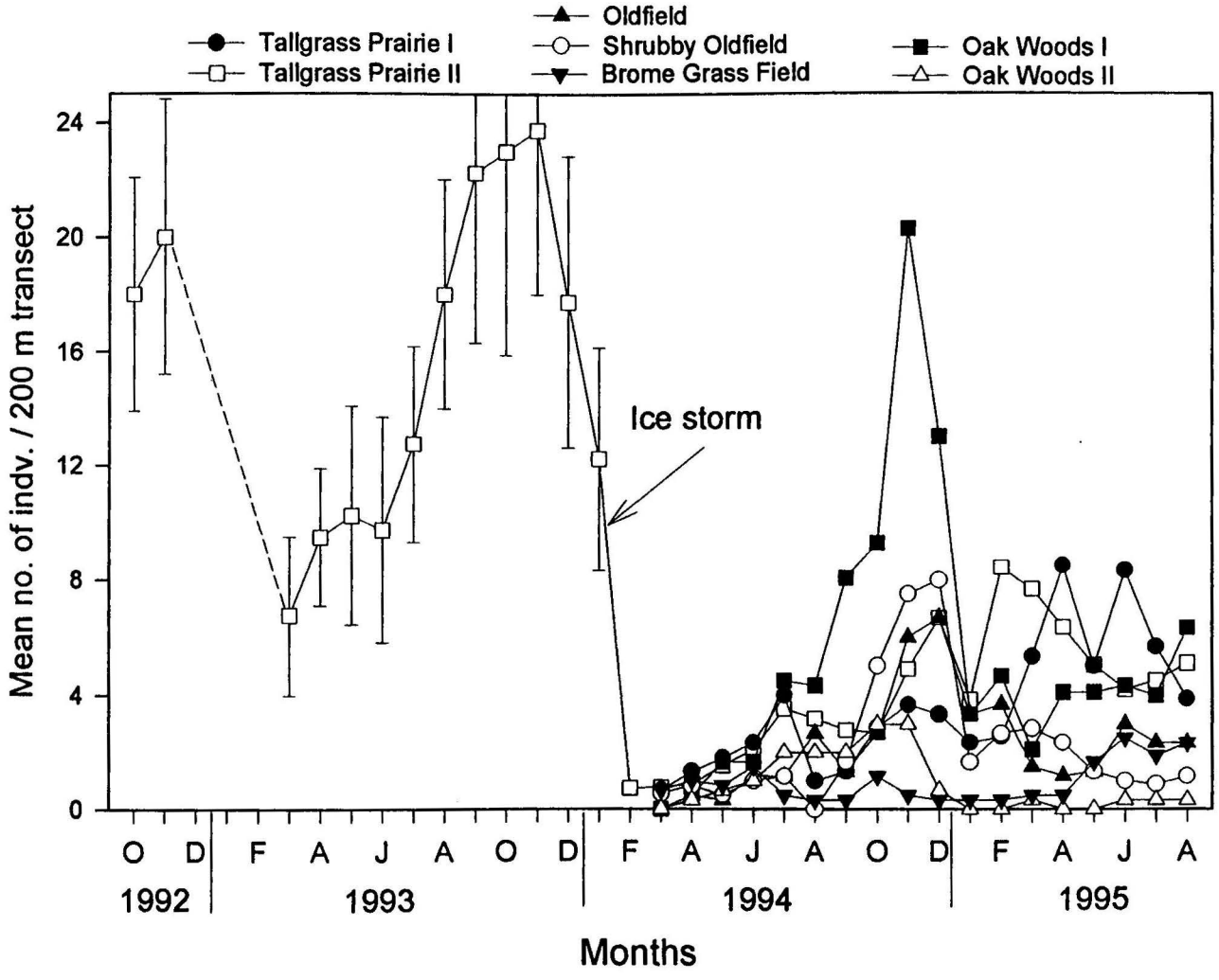

Figure 5. Numerical responses of small mammals at seven locations within Fermilab following the ice storm.

vertebrate prey at Fermilab (Sylvilagus, Peromyscus, and Microtus; Randa 1996, Cooper, unpublished data), Microtus showed the most protracted numerical response following the storm (Fig. 6). It was nearly 1½ years following the disturbance that voles began increasing in density. Within two years after the ice storm neither Microtus nor Peromyscus had returned to pre-storm densities (Fig. 4). It is unlikely that food was limiting the populations since densities were low. Also, a 23-year time series of precipitation showed that 1994 rainfall (and presumably plant productivity) was close to average (Fig. 7).

In addition to providing a unique abiotic disturbance, the ice storm effectively resulted in two distinct periods of population dynamics (i.e., pre- and post-storm). Accordingly, the effects of predator exclusion was analyzed prior to February 1994 and again during the corresponding time period in 1995/1996 following an increase in small mammal densities. However, the limited sample size in that latter time period precluded testing potential mechanisms.

At the initiation of small mammal trapping, M. pennsylvanicus densities were virtually identical on the control plots and the plots assigned to the predator exclosure treatment (Fig. 8a). During June and July of 1993 densities were greater on the plots assigned to predator exclusion. This may have been the result of intense human activity reducing vertebrate predator activity. For approximately 6 weeks prior to the completion of the exclosures, work was usually being conducted on the plots six days

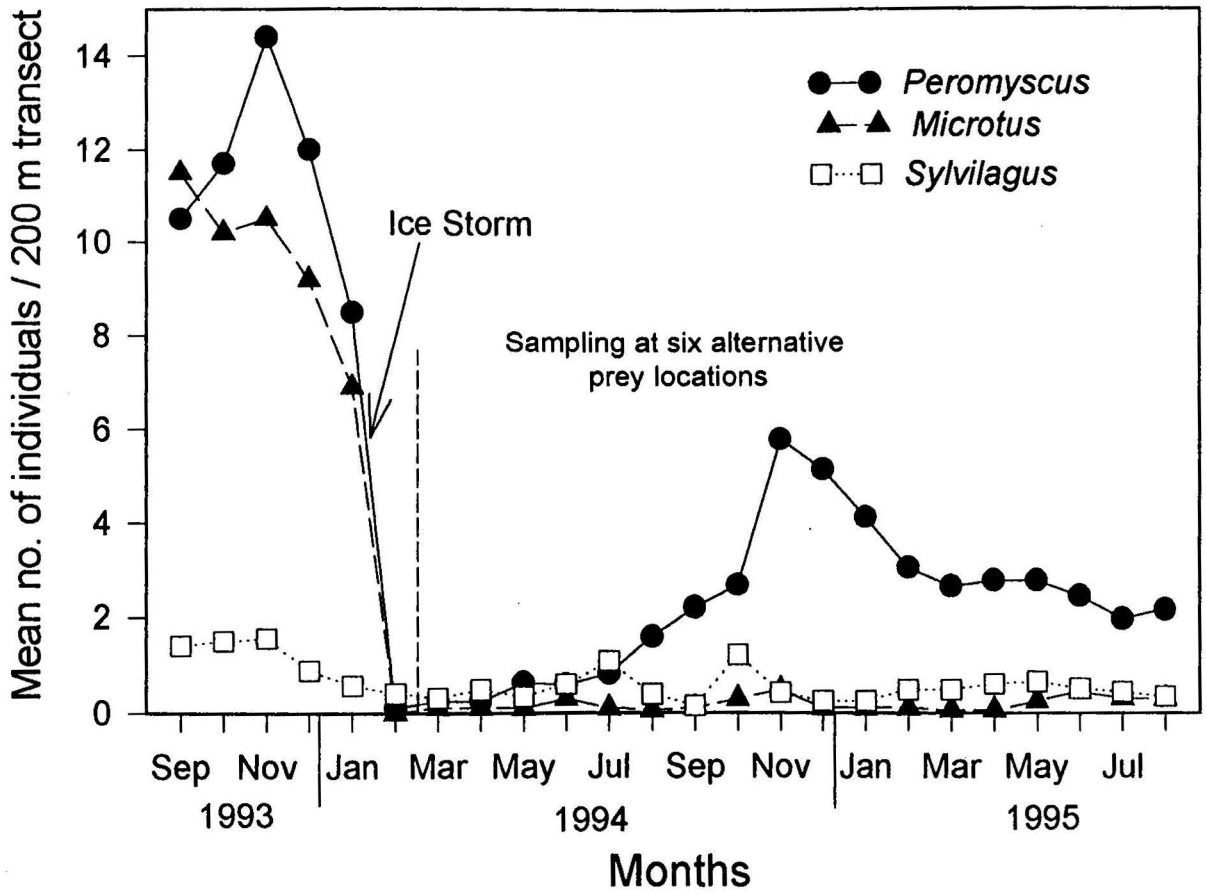

Figure 6. Numerical responses of the three most important vertebrate prey following the ice storm.

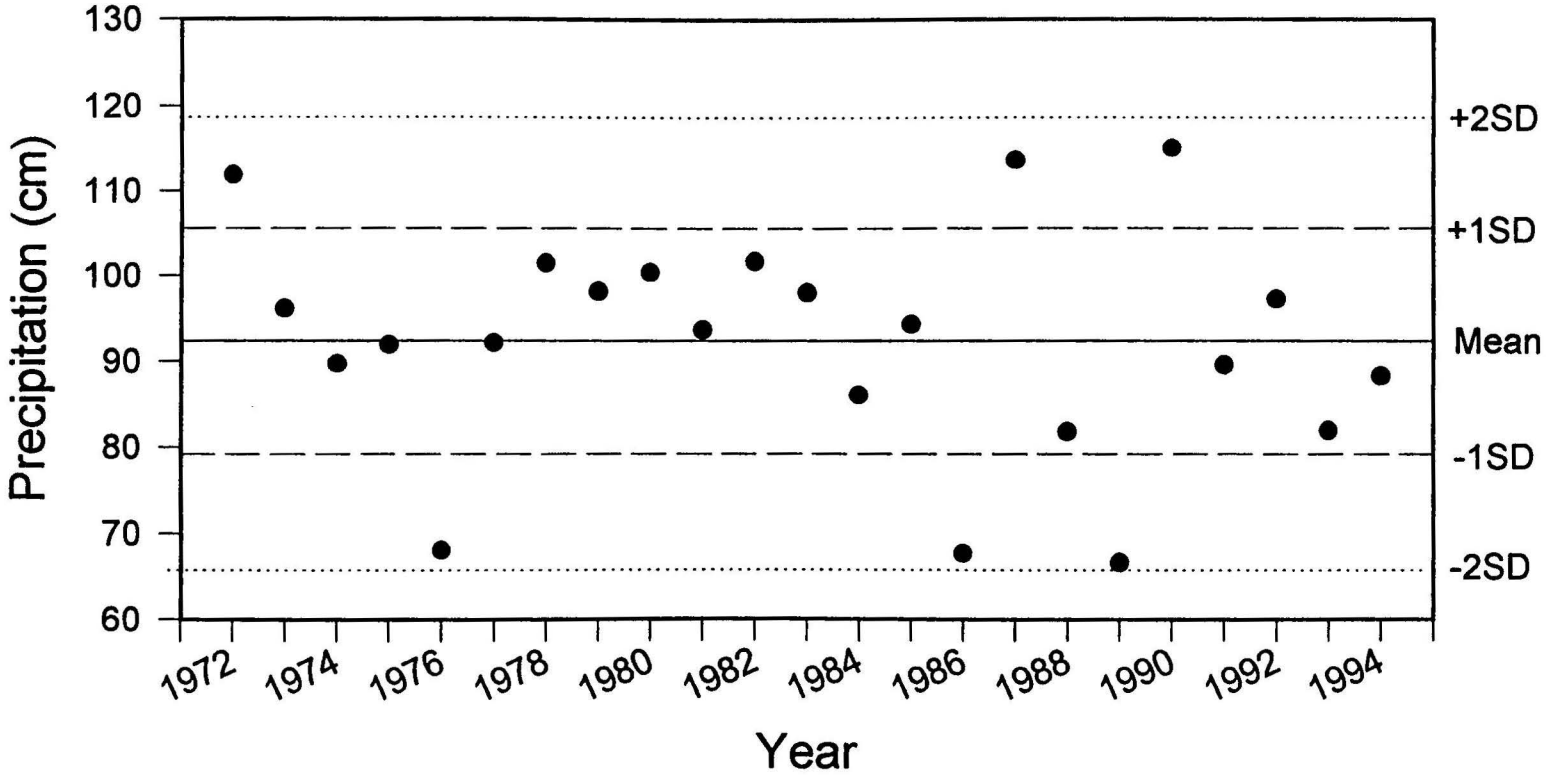

Figure 7. Twenty-three-year time series of precipitation at Fermilab.

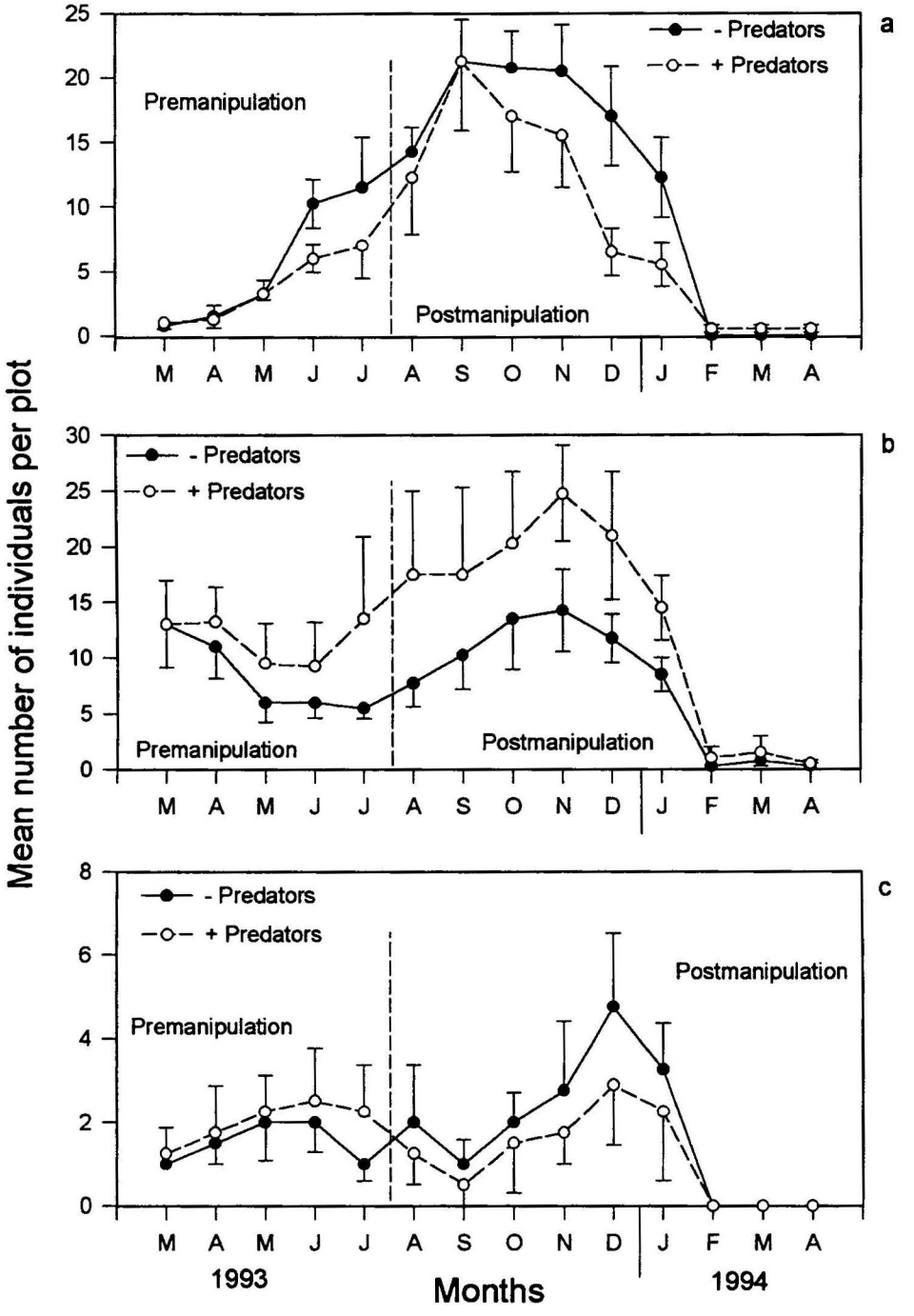

Figure 8. Pretreatment difference of small mammal densities (±1SE) on plots assigned to controls and predator exclusion and postmanipulation numerical responses. (a) Microtus pennsylvanicus, (b) Peromyscus leucopus, (c) Peromyscus maniculatus.

per week for up to 14 h per day. However, for the 3 months prior to the completion of the exclosures there was still no significant difference in densities ($F_{1,7} = 0.94$, $P = 0.370$). Following completion of the exclosures, the number of individuals increased, reaching a peak in September. Coinciding with the peak, the number of M. pennsylvanicus was virtually identical on the control and treatment plots. Subsequent to the peak, Microtus densities began to decline. The decline, however, occurred at a substantially greater rate on the predator access plots (Fig. 8a).

For M. pennsylvanicus, the Time x Predation interaction of the ANCOVA was not significant and subsequently removed from the full model. In the reduced model (Table 5), there was an overall significant effect of predator exclusion and significant Time and $Time^2$ terms. The latter two effects indicate that the number of M. pennsylvanicus changed significantly during the course of the investigation and that the change occurred as a quadratic response. That is, densities significantly increased, peaked, and subsequently decreased. Since there was an overall predator effect, individual t-tests were used qualitatively for post hoc comparisons to help objectively identify the months where differences were greatest. As is suggested by Fig. 8a, these were December 1993 and January 1994, at $P = 0.04$ and $P = 0.02$, respectively. Thus, immediately after M. pennsylvanicus reached its peak annual densities, terrestrial predators started to have a significant numerical effect, providing support for the generalist predator model. The effect was greatest two to three months following the peak.

Table 5

Analysis of covariance table for Microtus pennsylvanicus densities on predator vs. no predator plots during 1993-1994

Source	df	MS	F	P
Predation	1	256.687	5.48	0.0234
Time	1	407.059	8.69	0.0051
$Time^2$	1	473.357	10.11	0.0027
Error	44	46.835		

During the five months of premanipulation sampling, P. leucopus populations underwent a slight decline and subsequent increase, at which time densities were greater on the controls plots than the plots assigned to the predator exclusion treatment. The premanipulation increase continued until November, at which time populations began to decline. Although there was no statistically significant difference ($F_{3,4} = 3.038$, $P = 0.155$) in densities on the control plots vs. the plots assigned to the predator exclusion treatment, the premanipulation difference did continue throughout the duration of the study. However the difference became most pronounced during the decline (Fig. 8b).

As with M. pennsylvanicus, the interaction terms for the ANCOVA of P. leucopus densities were not significant and subsequently removed from the model. For the reduced model, there was an overall significant effect of predator exclusion on P. leucopus numbers and marginally significant Time and $Time^2$ terms (Table 6). However, some of the predation effect may be attributed to premanipulation differences (Fig. 8b). Again, the Time and $Time^2$ terms indicated a change in numbers over time and that the change occurred as a quadratic response (albeit a marginal one). Interestingly, the predator effect was opposite of the a priori prediction. That is, P. leucopus densities were actually greater on the predator access plots as compared to the exclusion plots. Using t-tests for post hoc multiple comparisons, the greatest difference was again during December 1993 and January 1994 (P=0.05 and P=0.07, respectively; Fig. 8b).

Table 6

Analysis of covariance table for Peromyscus leucopus densities on predator vs. no predator plots during 1993-1994

Source	df	MS	F	P
Predation	1	816.750	10.59	0.002
Time	1	291.717	3.78	0.058
$Time^2$	1	289.406	3.75	0.059
Error	44	77.154		

Premanipulation densities of P. maniculatus were relatively low, with mean numbers fluctuating between 1 and 2.5 individuals per plot (Fig. 8c). Following completion of the exclosures, densities increased, peaked in December, and subsequently declined. Both the increase and decrease occurred at a greater rate on the exclusion plots. Both the Time and $Time^2$ terms of the ANCOVA were significant, again confirming the significant increase and subsequent decrease (Table 7). There was also a marginally significant three-way interaction: Time x $Time^2$ x Predation. This shows that the number of P. maniculatus changed in a significantly different way on the control vs. predator exclusion plots over time and did so as a quadratic response.

Following the ice storm in 1994 and prior to the initiation of the food supplementation experiment in November, a total of 14 voles were captured, nine on the control plots and five on the exclusion plots. During this same time period very low densities of P. leucopus were present (Fig. 9). Although there was a significant increase in density over time, there was no indication of a predator exclusion effect (Table 8) .

Table 7

Analysis of covariance table for Peromyscus maniculatus densities on predator vs. no predator plots during 1993-1994

Source	df	MS	F	P
Predation	1	8.145	1.23	0.274
Time	1	26.352	4.42	0.042
$Time^2$	1	30.685	4.62	0.037
Time x Pred	1	8.706	1.31	0.259
$Time^2$ x Pred	1	9.276	1.40	0.244
Time x $Time^2$ x Pred	1	20.440	3.07	0.057
Error	40	6.647		

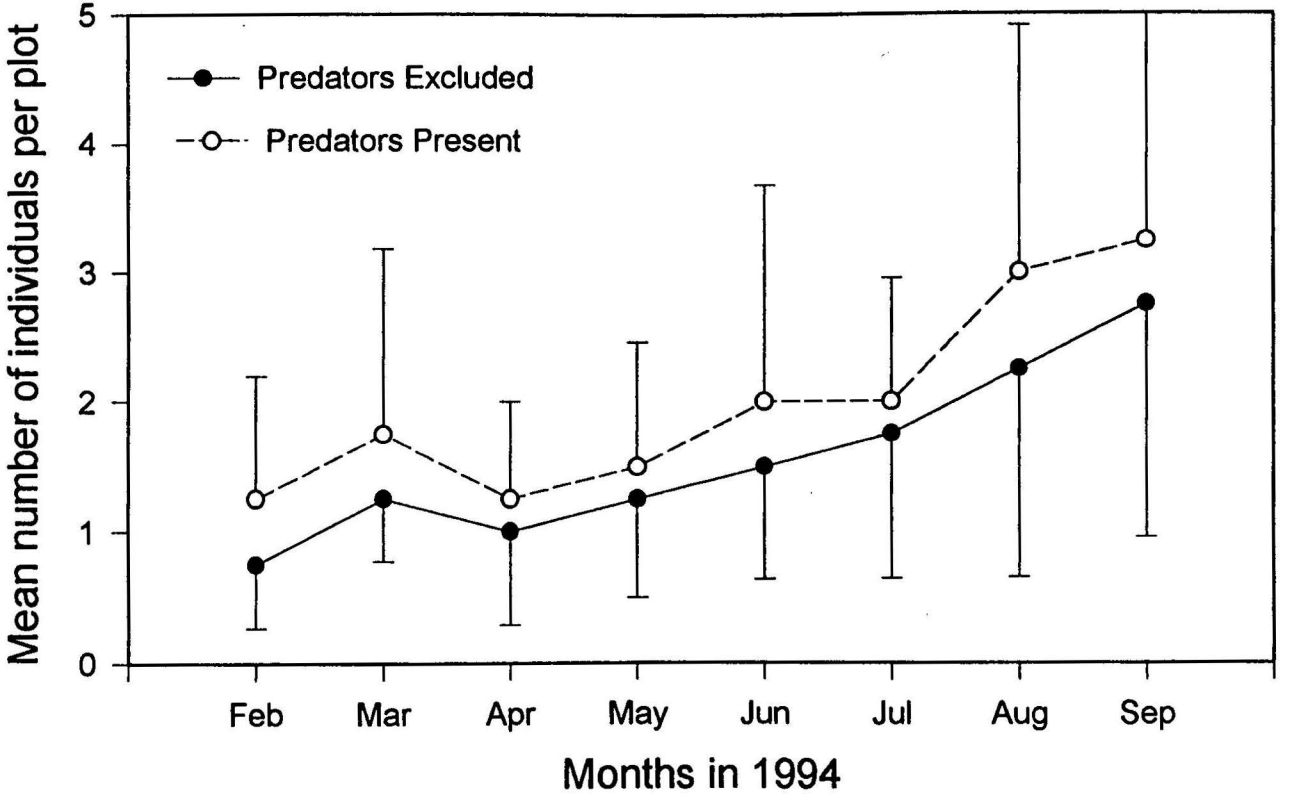

Figure 9. Peromyscus leucopus densities (±1SE) on predator exclusion and predator access plots during 1994.

Table 8

Analysis of Peromyscus leucopus densities on predator exclusion vs. predator access plots, February 1994 - October 1994.

Source	df	MS	F	P
Predation	1	2.053	0.40	0.528
Time	1	31.008	6.08	0.016
Time x Pred	1	1.408	0.28	0.601
Error	54	5.099		

The numerical responses of Microtus pennsylvanicus and Peromyscus leucopus to predator exclusion during 1995-1996 (Fig. 10) was similar in pattern to the 1993-1994 responses. Between May and August an average of 1-2 voles per month were present on the plots, regardless of treatment. This increased to just over four individuals on both the predator exclusion and predator access plots by September. On the controls, vole densities remained relatively constant into October, declined in November, and remained relatively constant throughout the remainder of the study. Densities on the predator exclusion plots peaked in October at an average of just over eight individuals per plots. The subsequent decline followed a pattern similar to the controls, although significantly greater densities persisted throughout the duration of the study (Table 9). The overall annual increase and subsequent decrease is reflected in the significant quadratic term.

Table 9

Analysis of covariance table for Microtus pennsylvanicus densities on predator vs. no predator plots during 1995-1996

Source	df	MS	F	P
Predation	1	256.687	5.48	0.0234
Time	1	407.059	8.69	0.0051
$Time^2$	1	473.357	10.11	0.0027
Error	44	46.835		

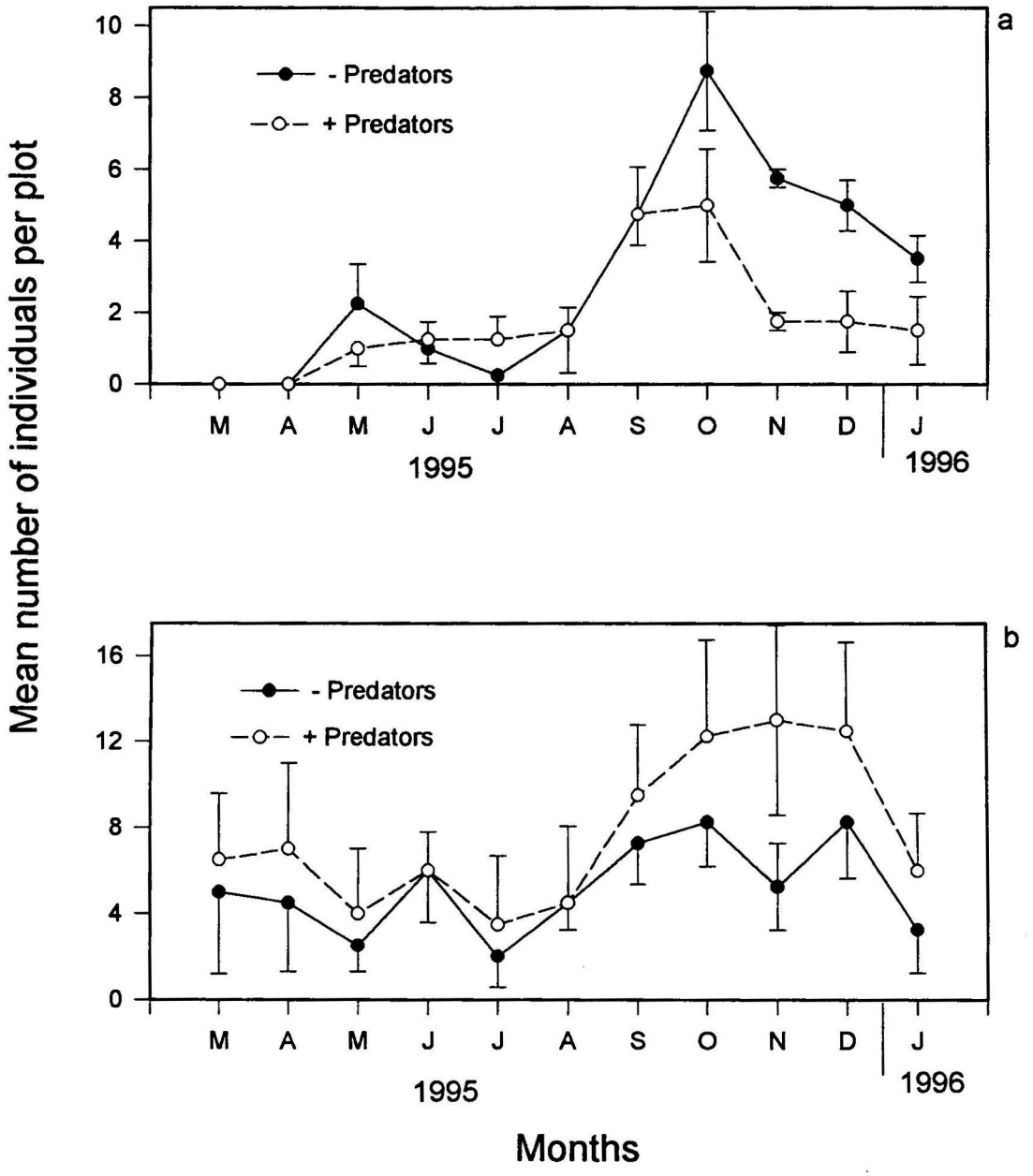

Figure 10. Small mammal densities (±1SE) on the predator exclusion and predator access plots during 1995-1996. (a) Microtus pennsylvanicus, (b) Peromyscus leucopus.

Between March and August, P. leucopus densities fluctuated between an average of three to seven individuals per plot (Fig. 10). Densities were similar on both the predator exclusion and predator access plots. On the predator exclusion plots, numbers increased slightly by October, following which there was no noticeable increase. Number decreased significantly by January. On the control plots, the number of P. leucopus increased significantly until October, following which they remained relatively constant until December. Densities declined significantly by December. As with Microtus, the annual increase and subsequent decrease accounted for the significant quadratic term (Table 10).

Table 10

Analysis of covariance table for Peromyscus leucopus densities on predator vs. no predator plots during 1995-1996

Source	df	MS	F	P
Predation	1	816.750	10.59	0.002
Time	1	291.717	3.78	0.058
$Time^2$	1	289.406	3.75	0.059
Error	44	77.154		

There was a significant change in M. pennsylvanicus body weights over time, the change occurring as a quadratic response (Table 11). There was also a significant Time x $Time^2$ x Predation interaction. When Microtus densities were near their peak, mean body weight was greater on the predator exclusion plots (Fig. 11a). This was followed by a rapid decrease in weights between October and November on the exclusion plots, resulting in the significant interaction.

Table 11

Analysis of covariance table for mean body weights of Microtus pennsylvanicus on predator vs. no predator plots over time

Source	df	MS	F	P
Predation	1	2.758	0.31	0.578
Time	1	151.108	17.25	0.001
$Time^2$	1	149.979	17.12	0.001
Time x Pred	1	3.142	0.36	0.552
$Time^2$ x Pred	1	3.434	0.39	0.535
Time x $Time^2$ x Pred	2	73.340	8.37	0.001
Error	39	99.411		

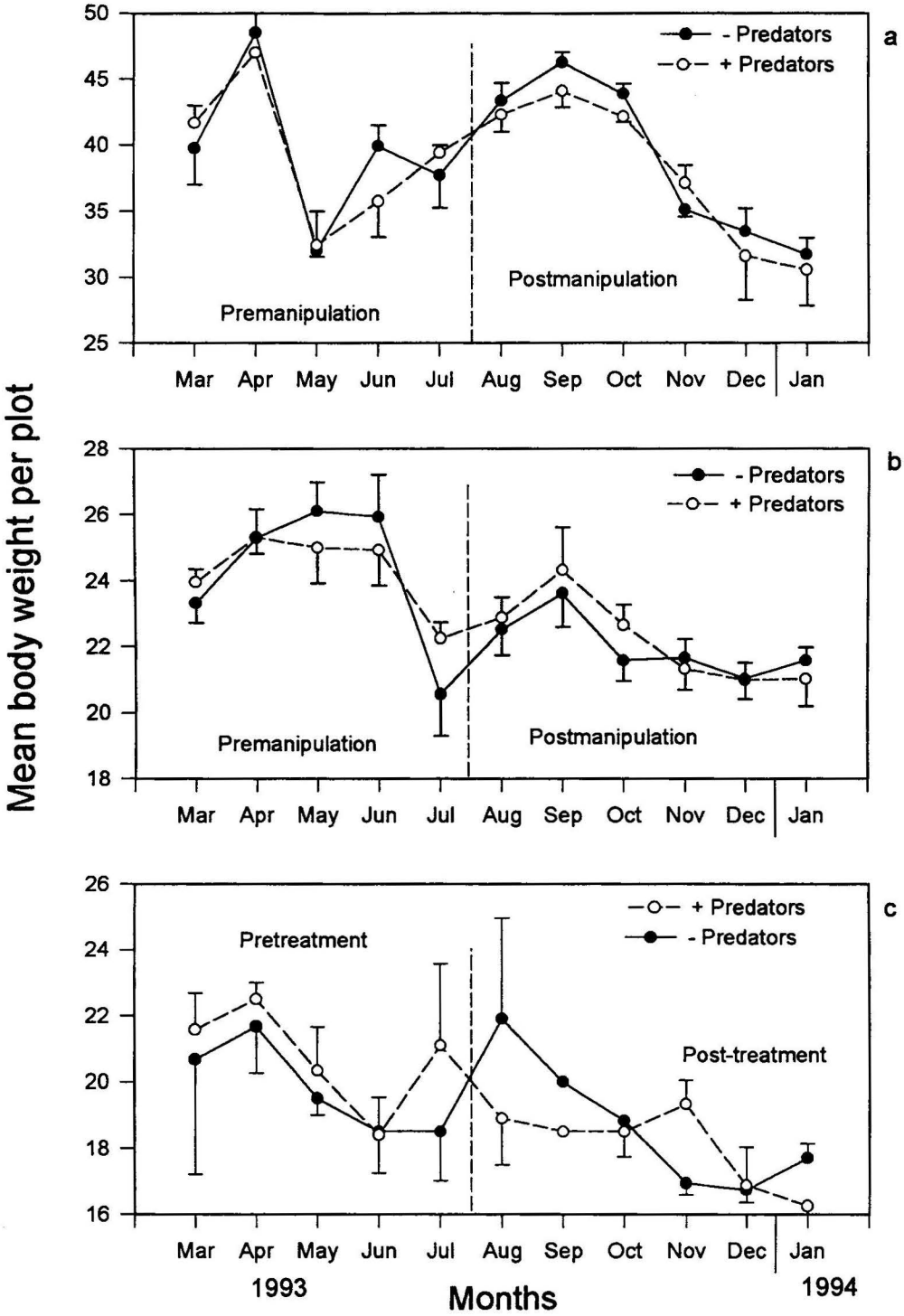

Figure 11. Mean small mammal body weights (±1SE) on the predator exclusion and predator access plots. (a) Microtus pennsylvanicus, (b) Peromyscus leucopus, (c) Peromyscus maniculatus.

For both P. leucopus and P. maniculatus there was a significant change in body weights over time (Tables 12, 13). However, unlike M. pennsylvanicus, the change was linear (without a significant quadratic term). Also, there was no indication of any significant predator exclusion effect on Peromyscus body weights (Fig. 11b, c).

Table 12

Analysis of covariance table for mean body weights of Peromyscus leucopus on predator vs. no predator plots over time

Source	df	MS	F	P
Predation	1	2.211	0.80	0.37
Time	1	31.303	11.32	0.001
Predation x Time	1	1.898	0.69	0.41
Error	44	2.765		

Table 13

Analysis of covariance table for mean body weights of Peromyscus maniculatus on predator vs. no predator plots over time

Source	df	MS	F	P
Predation	1	3.127	0.66	0.427
Time	1	40.453	8.53	0.008
Predation x Time	1	2.896	0.61	0.442
Error	23	4.740		

Overall survivorship of M. pennsylvanicus was extremely low (Fig. 12a). However, predator exclusion resulted in a significant increase in survivorship ($\chi^2 = 4.069$, df = 1, P = 0.044). Due to a large number of individuals only being captured during one trap session, the mean duration on the predator access plots was only 16.16 days, vs. 21.22 days on the exclusion plots. For both treatments, the maximum survival was 122 days.

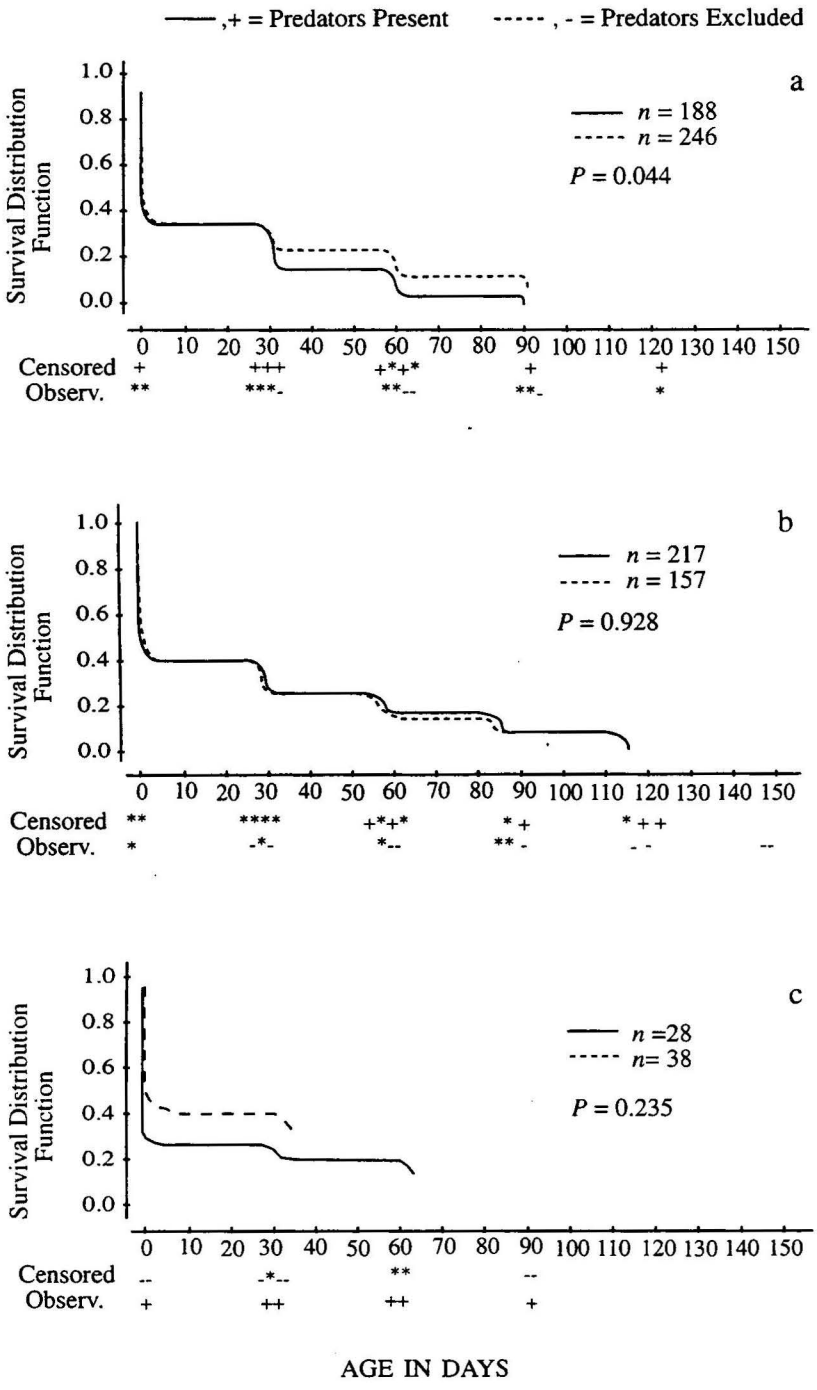

Figure 12. Survival distribution function, the probability of an individual age *t* having a lifetime exceeding *t*, on the predator exclusion vs. predator access plots. Below the abcissa, each symbol for a censored observation (i.e., right censored) represents an individual captured in the last trap session whose fate is unknown; an * indicates >1 individual. (a) Microtus pennsylvanicus, (b) Peromyscus leucopus, (c) Peromyscus maniculatus.

Peromyscus leucopus had somewhat greater overall survivorship than Microtus (Fig. 12b), although there was no significant effect of predator exclusion ($\chi^2 = 0.008$, df = 1, P = 0.928). The mean duration of P. leucopus survival on the predator access plots was 28.15 days and 27.31 days on the predator exclusion plots. For both treatments, the maximum survival was 148 days. As with P. leucopus, there was no significant effect of predator exclusion on P. maniculatus survivorship ($\chi^2 = 1.415$, df = 1, P = 0.235). However, the results must be interpreted with caution due to the limited sample size and short duration of occurrence of P. maniculatus on both the control (14.57 days) and exclusion (11.84 days) plots (maximum 90 days; Fig. 12c).

Sample size was not adequate for an analysis of P. maniculatus sex ratios, age structure, and reproduction, and was consequently limited to M. pennsylvanicus and P. leucopus. An ANCOVA of M. pennsylvanicus and P. leucopus percent subadults had significant Time and Time^2 effects (Tables 14, 15), indicating that for both species the proportion of subadults significantly increased, then subsequently decreased, during the postmanipulation period (Fig. 13). There was no indication of a significant predator exclusion effect on age structure of either species. However, for several months prior to the manipulation, the proportion of P. leucopus subadults was greater on the control plots (Fig. 13b). The direction of the effect was reversed immediately following the manipulation. When a doubly covariate analysis was used, with the proportion of subadults during July as the second covariate, there was an overall predator exclusion effect on P. leucopus age structure. That is, predator exclusion resulted in an increase in the proportion of young individuals.

Table 14

Analysis of covariance table for percent subadults of Microtus pennsylvanicus on predator vs. no predator plots over time

Source	df	MS	F	P
Predation	1	0.028	0.01	0.992
Time	1	1710.884	5.46	0.024
$Time^2$	1	1339.615	4.28	0.045
Pred x Time	1	3.044	0.01	0.922
Pred x $Time^2$	1	17.810	0.06	0.813
Error	42	313.239		

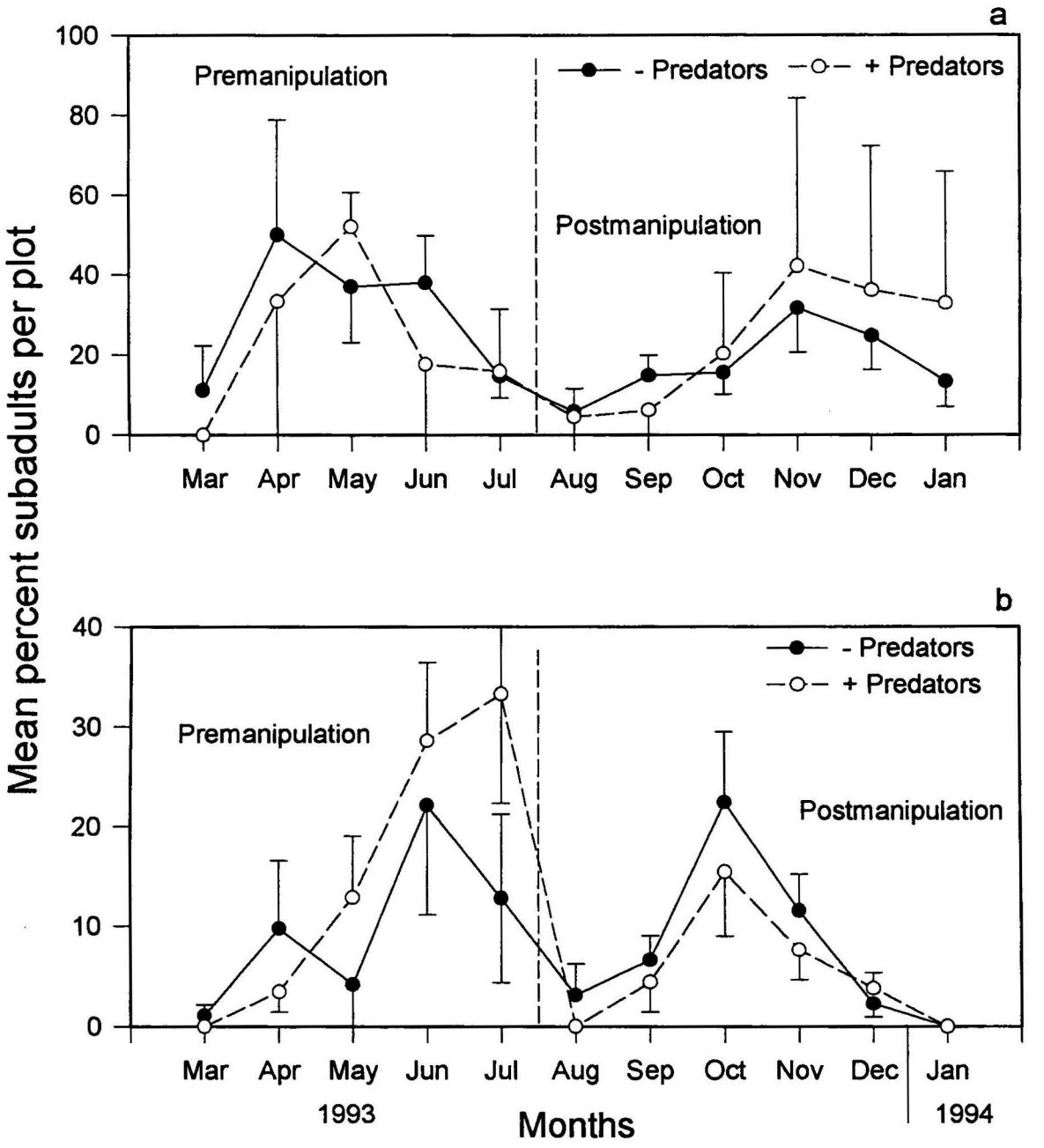

Figure 13. Percent subadults (±1SE) on the predator exclusion and predator access plots during 1995-1996. (a) Microtus pennsylvanicus, (b) Peromyscus leucopus.

Table 15

Analysis of covariance table for percent subadults of Peromyscus leucopus on predator vs. no predator plots over time

Source	df	MS	F	P
Predation	1	79.577	1.42	0.239
Time	1	1199.503	21.47	0.001
$Time^2$	1	1252.689	22.42	0.001
Pred x Time	1	12.769	0.22	0.641
Pred x $Time^2$	1	15.704	0.27	0.605
Error	44	55.868		

An ANCOVA of M. pennsylvanicus and P. leucopus sex ratios both had significant Time effects (Tables 16, 17); the proportion of female M. pennsylvanicus (Fig. 14a) decreased slightly, and the proportion of P. leucopus (Fig. 14b) females increased slightly, during the postmanipulation period (Table 17). There was no indication of any predator exclusion effect on the proportion of females for either species.

Table 16

Analysis of covariance table for Microtus pennsylvanicus sex ratios on predator vs. no predator plots over time

Source	df	MS	F	P
Predation	1	97.222	0.35	0.556
Time	1	1948.925	7.06	0.011
Predation x Time	1	51.183	0.19	0.669
Error	44	276.239		

Table 17

Analysis of covariance table of Peromyscus leucopus sex ratios on predator vs. no predator plots over time

Source	df	MS	F	P
Predation	1	95.992	0.65	0.423
Time	1	1422.103	9.69	0.003
Predation x Time	1	41.148	0.28	0.593
Error	44	146.809		

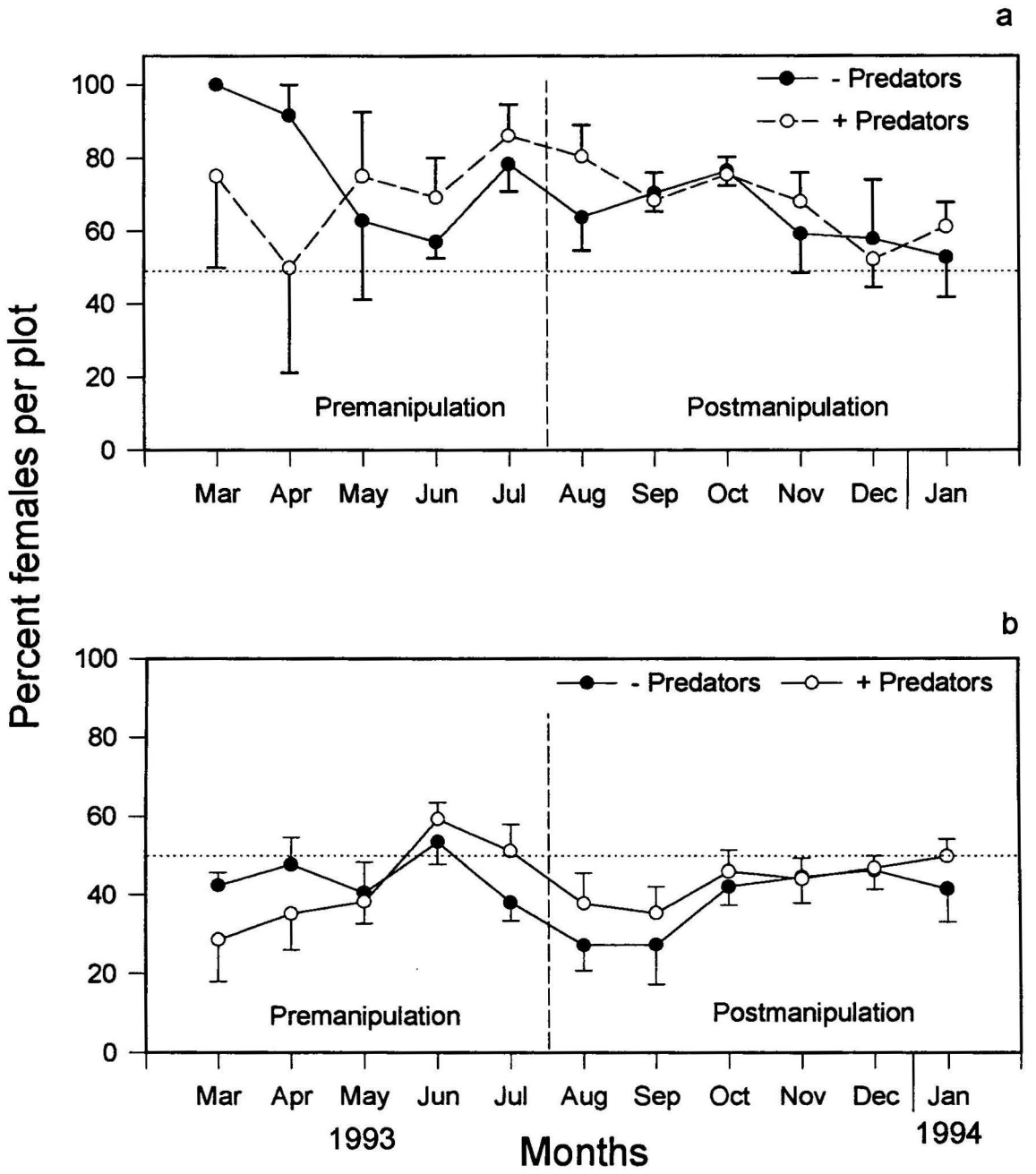

Figure 14. Sex ratios, expressed as percent females, (±1SE) on the predator exclusion and predator access plots during 1995-1996. (a) Microtus pennsylvanicus, (b) Peromyscus leucopus. The dotted line represents 50:50 sex ratios.

Similar to sex ratios, the only significant source of variation for the proportion of reproductively active female Microtus was Time (Table 18). At the start of the postmanipulation period, ca. 30% of the females were reproductively active (Fig. 15a). This proportion remained relatively constant through October, with reproduction having completely ceased by the November census. There was no indication of a significant predator exclusion effect on the proportion of reproductively active female Microtus. For P. leucopus, the proportion of reproductively active females changed significantly over time, steadily decreasing from the start of the postmanipulation period and ceasing in November (Fig. 15b). There was a significant effect of predator exclusion on P. leucopus and a marginally significant Predator x Time interaction (Table 19). However, the difference may be attributed to premanipulation differences. Using a doubly covariate ANCOVA, with the proportion of reproductively active females during July as the second covariate, there was no longer a significant predator exclusion effect.

Table 18

Analysis of covariance table of the proportion of reproductively active female *Microtus pennsylvanicus* on predator vs. no predator plots over time

Source	df	MS	F	P
Predation	1	2.223	0.01	0.910
Time	1	8277.516	47.56	0.001
Predation x Time	1	0.424	0.01	0.961
Error	44	174.154		

Table 19

Analysis of covariance table of the proportion of reproductively active female *Peromyscus leucopus* on predator vs. no predator plots over time

Source	df	MS	F	P
Predation	1	2660.280	5.18	0.028
Time	1	25834.760	50.29	0.001
Predation x Time	1	1879.497	3.66	0.062
Error	42	513.665		

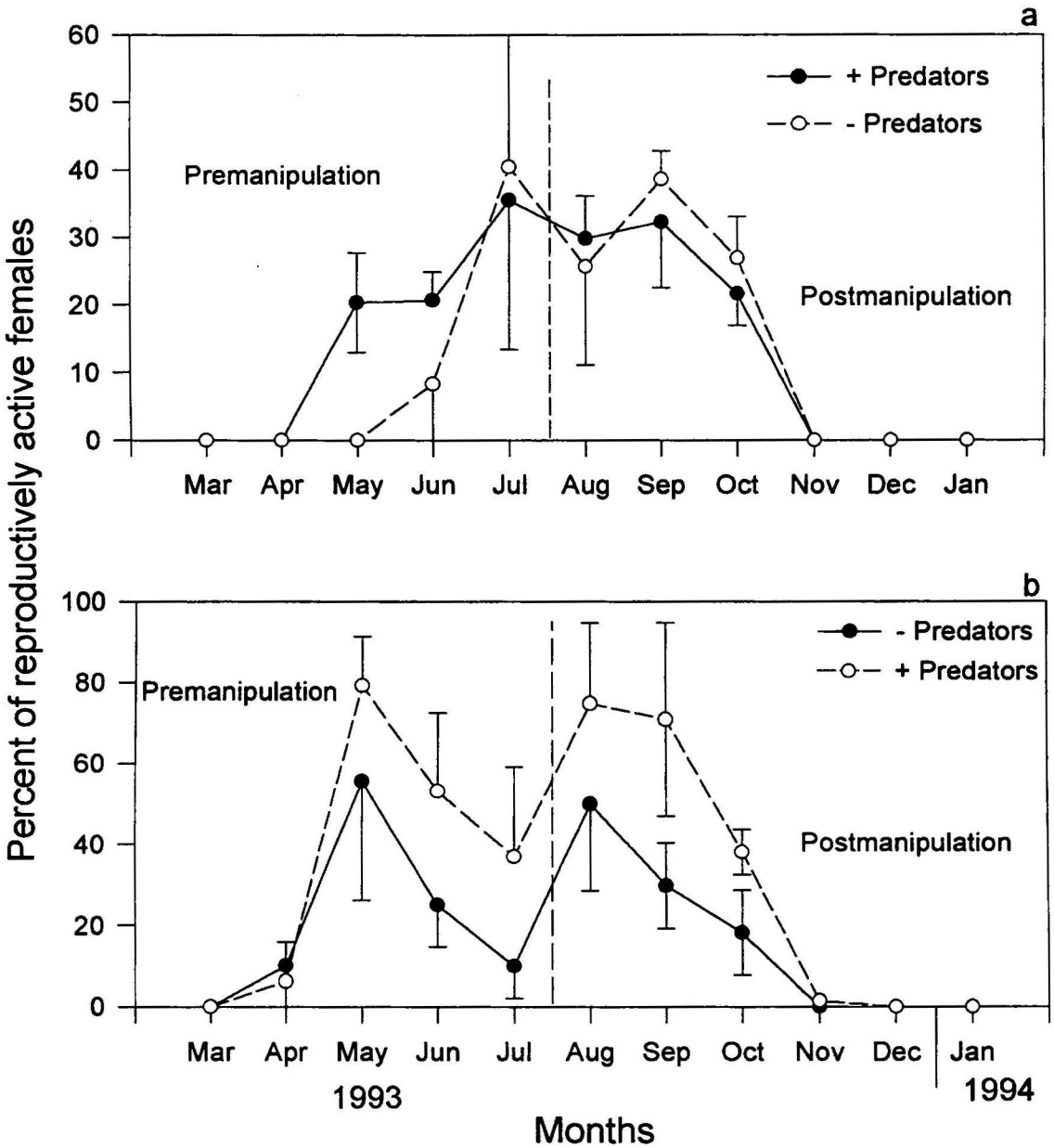

Figure 15. Percent of reproductively active females (±1SE) on the predator exclusion and predator access plots during 1995-1996. (a) Microtus pennsylvanicus, (b) Peromyscus leucopus.

Discussion

The number of small mammals declined dramatically following the severe ice storm in January 1994. The abrupt discontinuity in densities effectively resulted in two distinct periods of population dynamics, before and after the storm. During the first time period there were moderate to high densities of M. pennsylvanicus and P. leucopus. Terrestrial predator exclusion during the first time period resulted in a significant increase in Microtus densities. However, the effect did not occur while the population was undergoing an annual increase. Densities began to diverge on the control and treatment plots following an annual peak (i.e., October and November). The numerical response on the exclusion plots was corroborated by the predator diets. Randa (1996) concluded that the canids showed strong preferential selection for Microtus as compared to alternative prey. Also, the difference in densities became most pronounced during December and January. Female voles were reproductively active in October. However, by November reproduction had ceased. Thus, it appears that the strong predation intensity experienced by Microtus, when coupled with the cessation of reproduction and recruitment, resulted in a rapid decrease in densities due to predation.

A very similar pattern occurred during the second time period. Predators had a noticeable effect on Microtus when an annual peak in densities occurred in October. The effect became most pronounced in November and continued throughout the duration of the study. With only a one month difference in timing, the magnitude of

the effect in 1995-1996 was similar to 1993-1994. During the second time period, the experimental results were again corroborated by the analysis of the predator diets. Following the crash in rodents, predators significantly increased the proportion of Sylvilagus in their diets. However, as voles began to increase, so did their occurrence in the predators' diets (Randa 1996, Cooper, unpublished data). Thus, the results of the Microtus population dynamics provide support for Erlinge et al.'s (1984, 1988) generalist predator model. In heterogeneous landscapes, switching and preferential dietary selection by vertebrate predators can depress prey densities.

There was little or no support for mechanism (2) through (4) contributing to the increased vole densities on the exclusion plots. First, there was no indication of any predator exclusion effect on females, expressed as either a significant difference in sex ratios or proportion of reproductively active individuals. Consequently, mechanism (2) and (3) were not supported, suggesting that under natural conditions, female voles in estrous do not experience significantly greater rates of predation and that predators do not suppress female reproduction. Similarly, there was no support for mechanism (4), that predator exclusion and the subsequent reduction in foraging constraints imposed by predation risk, ultimately limited the procurement of food. Although body weights on the predator exclusion plots and predator access plots significantly converged and then diverged over time, there was no indication of overall body weight being greater in the absence of predators. That is, it did not appear individuals were eating more or expending less energy (i.e., not having to following "safe routes"; sensu Lagos et al. 1995) due to reduced constraints on movement. The most probable cause

for the increased Microtus densities on the predator exclusion plots was mechanism (1): a reduction in direct mortality due to predation resulted in increased survivorship. The increased survivorship resulted in a greater number of individuals.

On the predator exclusion plots vole numbers still declined. A probable explanation is the lack of adequate food. During both time periods, the decline began around the October-November trap censuses. The first heavy frost in 1993 was on October 10, and during 1995 on October 22. This frost was accompanied by a noticeable change in the vegetation, primarily turning brown and dying. Also, between mid-October and mid-December, 1993, a total of 34 voles were found dead in paths in and between the plots. Necropsy revealed little or no food in their stomachs.

What is less clear is why voles failed to increase during the summer of 1994. Three possible explanations, which are not necessarily mutually exclusive, are an inadequate food supply, the Allee effect (Allee 1938), and what Reid et al. (1995) have termed a "predator pit." The food supply hypothesis is an unlikely explanation. First, low densities suggest individuals would not have been able to deplete their food supply. Second, there was no reason to suspect food availability would have been particularly low since precipitation (and presumably plant productivity) during 1994 was close to average when compared to a 23-year time series. The Allee effect would be the result of densities following the ice storm being so low that individuals had difficulty in locating mates. The predator pit assumes that prey densities are so low that the prey are not able to break out of control by the predators. There is support for both of these hypotheses. If the predator pit hypothesis is correct, then a numerical

increase should have been observed on the exclusion plots during 1994. Since this did not occur, it suggests the Allee effect may be a plausible explanation. However, Randa (1996) showed that the canids were feeding on a substantially greater proportion of very young individuals following the ice storm, as opposed to prior to the storm. This suggests the "predator pit" hypothesis may be correct. That is, the vertebrate predators were feeding on young voles before most had the opportunity to reproduce. In all likelihood, both the Allee effect and predator pit hypothesis played a role in the protracted numerical response of M. pennsylvanicus following the ice storm.

During the first time period, neither P. leucopus nor P. maniculatus densities increased in response to predator exclusion. Rather, P. leucopus densities were lower on the predator exclusion plots. Although this difference may be partially attributed to pretreatment variation among the plots, the difference became most pronounced during November and January. This corresponds with the months when there was the greatest difference in Microtus densities between the predator exclusion and predator access plots. A very similar pattern was observed during the second time period. The months in which there was the greatest difference in vole densities between the controls and treatments corresponded with significantly lower Peromyscus densities on the predator exclusion plots as compared to the controls. Also, mice showed the greatest difference between controls and treatments (November) at the same time as voles, although the response was in opposite directions.

Numerous studies have documented an inverse correlation between densities of Microtus and of other small mammals (e.g., Blaustein 1980, R. megalotis, M. musculus, and M. californicus; Petticrew and Sadleir 1974, P. maniculatus and M. oregoni; Linzey 1984, Synaptomys cooperi and M. pennsylvanicus), including P. leucopus and M. pennsylvanicus (Wirtz and Pearson 1960). Three studies have experimentally investigated competition between Peromyscus and Microtus (Redfield et al. 1977; P. maniculatus and Townsend's voles (Microtus townsendii); Abramsky et al. 1979, P. maniculatus and M. ochrogaster; and Grant 1971, P. m. gracilis and M. pennsylvanicus). The lack of a predator exclusion effect on Peromyscus densities is corroborated by the lack of any significant effects on other demographic parameters. However, there is evidence that M. pennsylvanicus imposes changes in spatial patterns on P. leucopus (Chapter 4), resulting in the latter species having reduced numbers on the predator exclusion plots. Consequently, I suggest that interspecific competition, not predation, was at least partially responsible for determining P. leucopus densities. An alternative view is that predators do affect P. leucopus densities, but that it is an indirect effect mediated through Microtus.

Comparisons with other studies are difficult due to the limited number of field experiments and differences in experimental design. Desy and Batzli (1989) were able to clearly demonstrate that predators can limit M. ochrogaster densities. However, their experimental design involved the use of seeded populations on relatively small (0.13 ha) plots of nonnative grasses. At the end of 12 or 24 weeks, all individuals on the plots were removed and the experiment replicated in time. Consequently, it was

not possible to determine how predators affected naturally fluctuating population densities. Working in a semiarid region of northcentral Chile, Jaksic et al. (1993) showed that for the three most common species, the smallest (Akodon olivaceus) experienced relatively low levels of predation, the intermediate sized species (Phyllotis darwini) moderate levels of predation intensity, and largest of the three species (Octodon degus) relatively high level of predation. Numerical responses on the predator exclusion plots reflected the dietary analysis. Effects on A. olivaceus were negligible, P. darwini showed moderate and intermittent responses, while O. degus had extended and substantial increases in densities as a result of predator exclusion. This is similar to prairie. Predator effects on P. leucopus, the smaller of the two common species in this study, were negligible. M. pennsylvanicus, the larger of the two species, showed clear numerical effects to predator exclusion.

Finally, when overlaid against a background of large scale disturbance, the effects of predators on Microtus appear minimal. The ice storm significantly depressed numbers of M. pennsylvanicus and P. leucopus. Large scale disturbance may periodically "re-set" the system. Between such disturbances, predation, food availability, and competition may interact to determine Microtus and Peromyscus densities. Multifactorial experiments are needed to confirm these conclusions.

CHAPTER 4

BEHAVIORAL RESPONSES OF SMALL MAMMALS FOLLOWING VERTEBRATE PREDATOR EXCLUSION: A LARGE-SCALE FIELD EXPERIMENT

Introduction

Predators can affect their prey in a variety of ways. This can include not only numerical effects (Kerfoot and DeMott 1980, DeMott and Kerfoot 1982, Erlinge et al. 1983, Huffaker et al. 1984, Peckarsky 1985, Sih et al. 1985, Osenberg 1988, Gilliam et al. 1989, Riechert and Bishop 1990, Meserve et al. 1993, Meserve et al. 1996), but changes in a prey's behavior (Endler 1987, Brown 1988, Sih 1988, Lima and Dill 1990, Kotler et al. 1992, Lima 1992, Ylönen and Magnhagen 1992, Lagos et al. 1995, Yunger and Meserve, in review, Meserve et al., in prep.). During recent years, investigations on predation risk and microhabitat selection have helped to elucidate mechanisms of community structure (Brown 1989, Longland and Price 1991, Kotler et al. 1992, Yunger and Meserve, in review). In deserts, granivorous, quadrupedal rodents commonly feed under shrubs, sites of relatively low predation risk. Bipedal rodents, better adapted at detecting and escaping predators, utilize seed patches in the open. Thus, the effects of predators on prey behavior contributes to the coexistence of species utilizing the same resource (seeds; Brown 1989, Longland and Price 1991).

In streams, large grazing fish avoided shallow areas where they were more susceptible to predation by wading and diving predators; the large grazers were found primarily in deep pools (Powers 1987). Alternatively, small fish were most abundant in shallow portions of Panamanian and Oklahoma streams. Powers (1987) concluded that the small fish were less susceptible to avian and mammalian predators and more susceptible to predation by large picivorous fish found in deep pools.

In contrast to the work on microhabitat selection, the effects of predators on the movement and spatial behavior of prey has received relatively little attention (but see Desy et al. 1991, Lagos et al. 1995). Predation risk may constrain the distance prey move: the more mobile an individual the greater the probability of it being detected by a predator. Constraints on movement may influence social structure by reducing individual home range size and home range overlap between individuals. An alternative hypothesis is that if individuals preferentially exploit microhabitats with reduced predation risk, movements could increase as a result of traveling between specific locations. In turn, this would increase individual home range size and overlap between individuals.

Data on small mammal trap records collected between March 1993 and January 1994 were used to address the question: How does predation risk alter individual movement, home range size, and home range overlap between individuals? Unlike arid systems, where the role of predation risk on microhabitat selection has been well studied, prairie does not have distinct "open" and "covered" sites between which individuals can selectively move. Consequently, I predicted that (1) predation risk

would reduce the distance an individual moves, (2) this would in turn reduce individual home range size and home range overlap between individuals, and (3) at a large spatial scale (i.e., not microhabitat), individuals would move in a non-random fashion toward areas of reduced predation risk. The above three questions were addressed using the white-footed mouse (Peromyscus leucopus). Due to limited sample size and limited distances moved, only questions (1) and (2) were tested with the meadow vole (Microtus pennsylvanicus) and question (1) with the prairie deer mouse (Peromyscus maniculatus).

Data Analysis

The distance an individual moved was expressed as mean distance between successive captures (MDBSC). MDBSC was calculated using the home range subroutine of the program Capture-Mark-Recapture (CMR) (Le Boulengé 1987). March through July constituted a premanipulation period, August through January the postmanipulation period. Treatment effects were tested with an ANCOVA using SAS PROCEDURE GLM (SAS 1990a). The premanipulation period was used as the covariate to remove pre-existing differences between control and predator exclusion plots.

To calculate the area of individual home ranges, the location of capture records were transcribed onto a 50 x 50-cm diagram of the plots, with individual grid stations positioned to scale. Home range area was calculated only for individuals with ≥5 captures. SigmaScan (Jandel Scientific 1988) was used to digitize the boundary of

individual home ranges following the criteria of the exclusive boundary strip method (Stickel 1954). For my grids, this results in 36, 12 x 12-m squares with the grid stations positioned in the middle of each square. The corners of the squares are connected assuming the most direct route between capture locations. There are numerous methods for calculating home range area and several programs that implement these methods. Extensive debate has focused on the most appropriate method and most useful software packages (Boulanger and White 1990, Larkin and Halkin 1994). However, due to the difficulty in programming the algorithms for implementing the exclusive boundary strip method, it has not been incorporated in software packages or discussed in reviews of home range techniques. Though computationally laborious, the exclusive boundary strip method provides accurate estimates of home range size (Stickel 1954). It is particularly useful for small sample sizes and data collected using grids with regular intervals (i.e., unlike alternative techniques, it does not assume a particular underlying distribution or sample size [Jennrich and Turner 1969, Dixon and Chapman 1980, Anderson 1982]). Also, for purposes of this investigation, a precise estimate of the true home range size is not essential. Rather, the focus is whether a difference exists between the estimated home range size of the control and treatment plots.

Smith and Ivin's (1983) weighted overlap program was used to calculate pairwise comparisons of percent home range overlap between individuals. This was done for both inter- and intraspecific comparisons. The weighting has the advantage that it takes into account the number of times an individual is captured at a particular

location. For example, two individuals, each captured one out of ten times at the same location, would each have a 10% overlap; two individuals each captured five out of ten times at the same location, would each have a 50% overlap, even though both sets of individuals could potentially have the same home range area. Changes in overlap within a species were analyzed with an ANCOVA using the procedure applied to MDBSC. Interspecific comparisons were analyzed using a one-way ANOVA.

Inter-grid movements were relatively rare and only P. leucopus had an adequate sample size for statistical analysis. Intergrid movements were calculated in four directions between adjacent, consecutive months: (+P = predator access; -P = predator exclusion) +P → +P, +P → -P, -P → +P, -P → -P. As with the MDBSC calculations, March through July constituted a premanipulation period and August through January the postmanipulation period. Treatment effects were tested using a likelihood ratio chi-square with SAS PROCEDURE FREQ (SAS 1990b). Premanipulation data were used to calculate the expected values and postmanipulation data to calculate the observed values.

Results

There was no significant effect of predator exclusion on MDBSC of M. pennsylvanicus, either main effects or interactions (Table 20, Fig. 16a). For P. leucopus, MDBSC was significantly greater on the predator exclusion plots as compared to the controls (Table 21). The significant effect, however, was due to premanipulation differences (Fig. 16b); there was no significant time of manipulation x

Table 20

Analysis of variance table for Microtus pennsylvanicus mean distance between successive captures on predator vs. no predator plots for premanipulation vs. postmanipulation

Source	df	MS	F	P
Predation	1	0.596	0.05	0.834
Pre vs. Post Treatment	1	1.055	0.09	0.782
Pred x Pre vs. Post	1	0.380	0.03	0.867
Error	4	11.502		

Table 21

Analysis of variance table for Peromyscus leucopus mean distance between successive captures on predator vs. no predator plots for premanipulation vs. postmanipulation

Source	df	MS	F	P
Predation	1	53.045	7.43	0.052
Pre vs. Post Treatment	1	1.248	0.17	0.697
Pred x Pre vs. Post	1	0.008	0.01	0.974
Error	4	28.573		

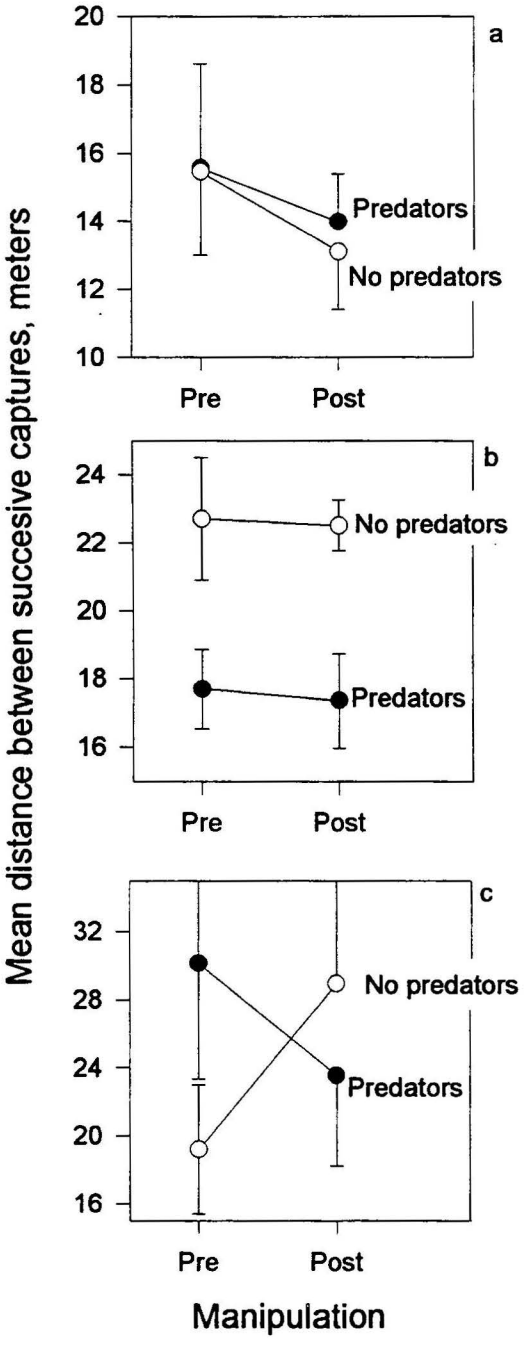

Figure 16. Mean distance between successive captures of (a) Microtus pennsylvanicus, (b) Peromyscus leucopus, and (c) Peromyscus maniculatus.

predator interaction (Table 21). For P. maniculatus, there was a marginally significant predator exclusion effect and time of manipulation vs. treatment interaction (Table 22, Fig. 16c). The interaction, in particular, indicated predators had a weak effect on the MDBSC for P. maniculatus; the predator exclusion resulted in increased movement.

There was not an adequate premanipulation sample size for the inclusion of a covariate for the analysis of M. pennsylvanicus home range size. Consequently, a t-test was used to compare predator exclusion vs. predator access plots (Fig. 17a). There was no significant difference in home range size between the controls vs. treatments ($t = 0.9103$, $df = 6$, $P = 0.3978$). For P. leucopus, there was a significant overall predator effect and a significant time of manipulation x predator interaction (Table 23). The interaction shows that predator exclusion results in a significant decrease in P. leucopus home range size (Fig. 17b).

As with home range, there was not an adequate premanipulation sample size for the inclusion of a covariate for the analysis of M. pennsylvanicus home range overlaps. Consequently, a t-test was again used to compare predator exclusion vs. predator access plots (Fig. 18a). There was no significant difference in home range overlap between the controls vs. treatments ($t = 0.8617$, $df = 6$, $P = 0.4219$). For P. leucopus, there was again a significant time of manipulation x predator interaction (Table 24). The predator exclusion resulted in increased overlap between individual home ranges (Fig. 18b).

Table 22

Analysis of variance table for Peromyscus maniculatus mean distance between successive captures on predator vs. no predator plots for premanipulation vs. postmanipulation

Source	df	MS	F	P
Predation	1	175.326	62.51	0.080
Pre vs. Post Treatment	1	149.740	53.59	0.086
Pred x Pre vs. Post	1	170.684	60.86	0.081
Error	4	2.805		

Table 23

Analysis of variance table of home range size for Peromyscus leucopus on predator vs. no predator plots for premanipulation vs. postmanipulation

Source	df	MS	F	P
Predation	1	353879.240	12.28	0.004
Pre vs. Post Treatment	1	779.666	0.03	0.872
Pred x Pre vs. Post	1	138564.479	4.81	0.048
Error	12	838987.234		

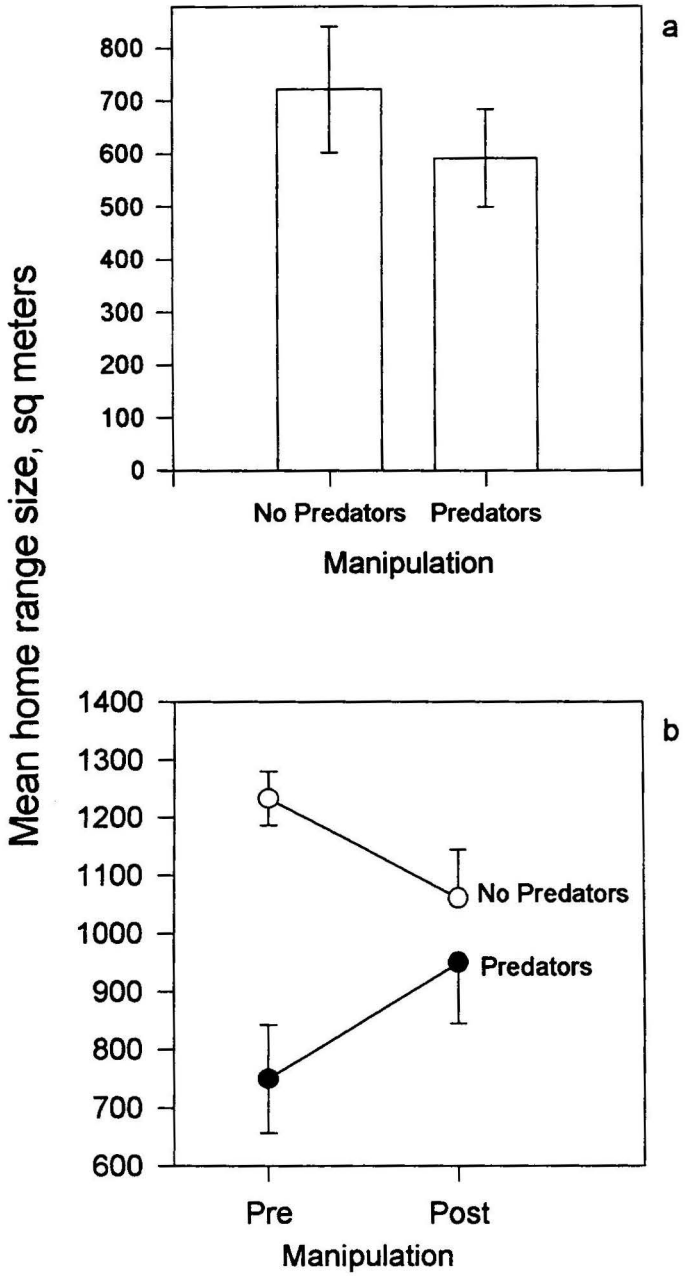

Figure 17. Mean (±SE) home range, in square meters, for (a) Microtus pennsylvanicus and (b) Peromyscus leucopus.

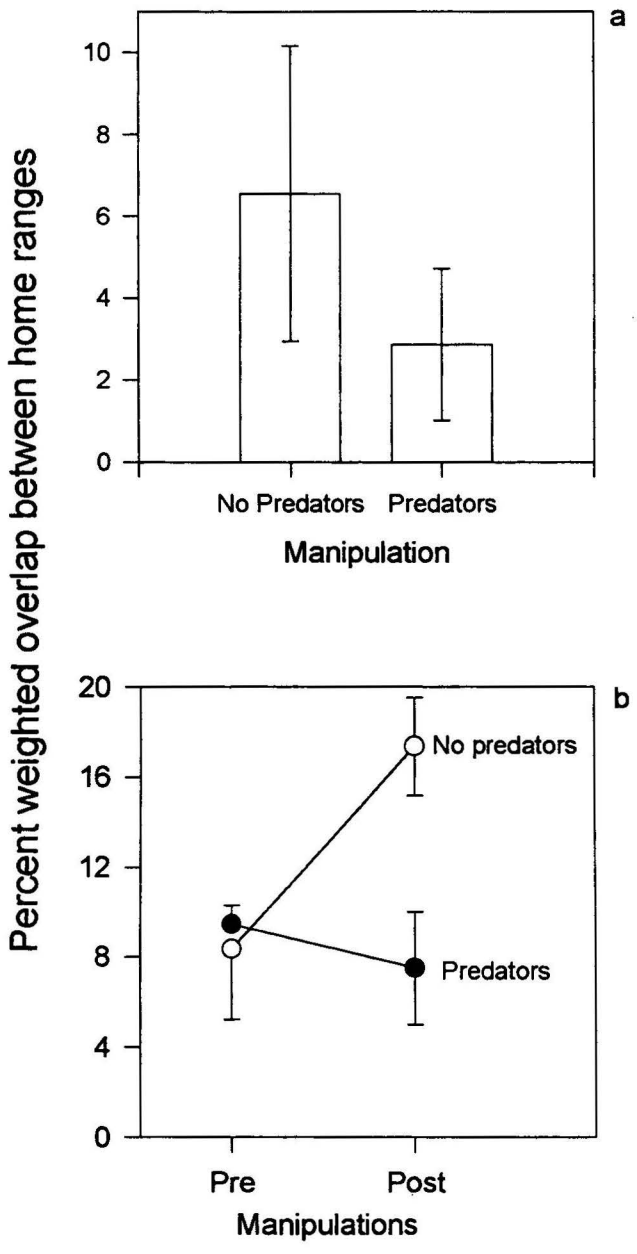

Figure 18. Means (±SE) of percent weighted overlap between home ranges for (a) Microtus pennsylvanicus and (b) Peromyscus leucopus.

Table 24

Analysis of variance table of home range overlaps for Peromyscus leucopus on predator vs. no predator plots for premanipulation vs. postmanipulation

Source	df	MS	F	P
Predation	1	76.562	3.56	0.082
Pre vs. Post Treatment	1	49.632	2.31	0.154
Pred x Pre vs. Post	1	121.000	5.63	0.035
Error	12	21.487		

There was an overall significant difference in inter- vs. intraspecific home range overlap between Microtus and Peromyscus ($F_{2,9} = 4.85$, $P = 0.0372$; Fig. 19). A Student-Newman-Keuls multiple comparison (Winer et al. 1991) showed that there was no significant difference between the Microtus-Microtus and Microtus-Peromyscus comparison; however, the Peromyscus-Peromyscus comparison was significantly greater than the two previous comparisons. That is, P. leucopus had lower interspecific overlaps as compared to intraspecific overlaps in home range. Peromyscus leucopus also showed a significant difference in directional movements between grids ($\chi^2 = 9.692$, df = 3, $P = 0.021$). An a posterior test showed the difference was due to postmanipulation movement between predator exclusion plots (Table 25).

Discussion

Contrary to initial predictions, the exclusion of predators had no significant effect on M. pennsylvanicus MDBSC, home range size, or home range overlaps. It is unlikely that the voles were simply "unaware" that predators were absent. All carnivores produce pungent odor (Macdonald 1980). Rodents, including Microtus, can detect such odors and respond by reducing their activity in locations where carnivores have recently been active (Stoddart 1976, Gorman 1984, Sullivan et al. 1988). However, this study suggests that predators do not influence M. pennsylvanicus spatial patterns.

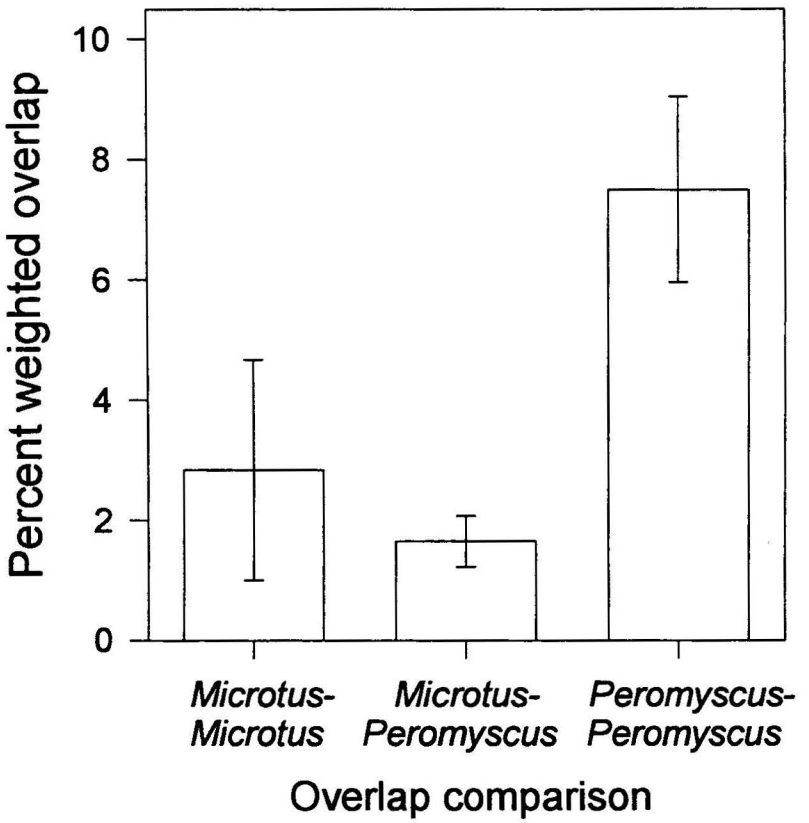

Figure 19. Mean (±SE) percent weighted overlaps between M. pennsylvanicus and M. pennsylvanicus, M. pennsylvanicus and P. leucopus, and P. leucopus and P. leucopus individuals on control plots.

Table 25

Number of between plot movements (predator [+P] vs. no predator [-P]) for Peromyscus leucopus during pre- and postmanipulation periods

	Treatment			
Treatment period	+P → +P	+P → -P	-P → +P	-P → -P
Pre	3	11	12	0
Post	2	12	10	7

During the investigation, Microtus was under strong predation pressure. Randa (1996), working with coyotes (Canis latrans) and red fox (Vulpes vulpes), and Cooper (unpublished data), working with Great-horned Owls (Bubo virginianus) and Red-tailed Hawks (Buteo jamacensis), concluded that the predators showed a strong preferential selection for Microtus, regardless of overall prey availability. Following an annual peak in density, the preferential selection of voles by predators significantly reduced Microtus densities. These results were repeated during two separate years with a one-year interval, clearly demonstrating predators have a numerical effect on M. pennsylvanicus (Chapter 4). This numerical effect could have potentially confounded the spatial data. Trap records used in calculating MDBSC and home range size were from a time period when densities were greater on the exclusion plots. Previous work,

including studies on M. pennsylvanicus, have shown that if density affects home range size, it is an inverse correlation (Getz 1961, Van Vleck 1969, Maza et al. 1973, Abramsky and Tracy 1980, Gaines and Johnson 1982). That is, as density increases, home range size decreases. Consequently, the increase in density could have potentially "off-set" any change in spatial patterns resulting from reduced predation risk.

Work with a caviomorph rodent in northcentral Chile, the degu (Octodon degus), has shown that it is under strong predation intensity (Jaksic et al. 1993). As with M. pennsylvanicus, this predation intensity resulted in numerical increases following vertebrate predator exclusion (Meserve et al. 1996). However, unlike M. pennsylvanicus, predator exclusion affected O. degus movements (Lagos et al. 1995). The area of daily movements was significantly smaller, and runways, which were not as straight, traversed open areas more often in the absence of predators. Lagos et al. (1995) concluded that a reduction in the perceived risk of predation resulted in individuals moving throughout open area more "thoroughly" and the subsequent need for a smaller home range. They did not, however, take into account the significantly greater densities of O. degus resulting from predator exclusion (Meserve et al. 1996); increases in density have repeatedly been shown to be correlated with decreases in home range size (Getz 1961, Van Vleck 1969, Maza et al. 1973, Abramsky and Tracy 1980, Gaines and Johnson 1982).

Desy et al. (1990) studied seeded populations of prairie voles (M. ochrogaster) in a central Illinois bluegrass field. Using replicated 0.13-ha plots, they detected a

significant increase in vole densities and survival at the end of 24 weeks as a result of predator exclusion. The investigators were able to demonstrate a significant increase in vole home range size on the exclusion plots. They concluded that predators can inhibit the movements of M. ochrogaster.

The two previous studies recorded changes in spatial patterns, presumably due to a reduction in predation risk, following numerical responses of the prey to predator exclusion. Why this did not apply to M. pennsylvanicus in the current study is unclear. One possible explanation is that resources, not predation, are responsible for determining M. pennsylvanicus home range size. A model proposed by Ostfeld (1985, 1990) predicted that food is the resource defended by female small mammals and that females are the resource defended by males. There are several studies that support the model (see Ostfeld 1985, 1990), although results from other investigations are equivocal (Wolff and Cicirello 1989, Madison 1980).

Predator exclusion resulted in a marginally significant change in the MDBSC of P. maniculatus. This provides limited support for the a priori prediction of predation risk reducing small mammal movements. That is, in the absence of predators, there is a reduced probability of being detected and captured by a predator associated with increased movement. However, there was not a significant change in the MDBSC of P. leucopus. There was a significant decrease in home range size and a significant increase in home range overlaps between P. leucopus individuals when predators were excluded. The predator manipulation also significantly affected intergrid movements of P. leucopus: following the manipulation there was a significant increase in

movement between the predator exclusion plots. Consequently, the a priori prediction of predation risk reducing movement of P. leucopus was not supported. The significant decrease in P. leucopus home range size was opposite of the a priori prediction, while the significant increase in home range overlaps fits the prediction.

A possible explanation for the conflicting spatial movement results of predators on Peromyscus is a lack of predation intensity. Contrary to Microtus, the presence of Peromyscus in the vertebrate predator diets was somewhat below what was predicted based on naturally occurring prey abundances (Randa 1996, Cooper, unpublished data). This would suggest that Peromyscus is not under strong selective pressure from predation, at least not when compared to Microtus. In fact, P. leucopus densities were significantly lower on the predator exclusion plots as compared to the controls (see Chapter 4). Part of the numerical response may be attributed to premanipulation differences. However, as compared to the controls, P. leucopus densities were lowest on the exclusion plots when M. pennsylvanicus showed the largest difference between treatments and controls.

Numerous studies attest to the competitive effects of Microtus on Peromyscus (e.g., Wirtz and Pearson 1960, Petticrew and Sadleir 1974, Redfield et al. 1977, Abramsky et al. 1979, Grant 1971, Chapter 2). Both inverse correlations in spatiotemporal patterns of density and removal experiments have shown Microtus can significantly reduce Peromyscus densities and even result in competitive exclusion; this includes both M. pennsylvanicus and P. leucopus (Wirtz and Pearson 1960). Thus, M. pennsylvanicus could be directly responsible for the significant changes in P. leucopus

movement. Specifically, the decrease in home range size would reduce the probability of P. leucopus encountering M. pennsylvanicus and subsequent antagonistic encounters. This would also explain the significant increase in overlaps. To avoid interspecific encounters, Peromyscus increase their activity in locations where Microtus are less active. This conclusion is supported by the inter- vs. intraspecific overlap comparisons. Microtus pennsylvanicus had a relatively low degree of intraspecific overlap; P. leucopus had a significantly higher degree of intraspecific overlap. However, the low degree of interspecific home range overlap indicated avoidance of Microtus by Peromyscus, providing support for the effects of Microtus on Peromyscus spatial patterns.

Following completion of the predator exclosures, Peromyscus leucopus movements between +P→ +P, +P→ -P, and -P→ +P remained relatively constant as compared to premanipulation movements. The significant increase in -P→ -P intergrid movements may be partially explained by antagonistic encounters with Microtus: as Microtus densities increase, so does the exodus of Peromyscus. What remains unclear is why these individuals moved to other exclusion plots.

In conclusion, predation appeared to have relatively little effect on M. pennsylvanicus spatial patterns and movement in northern Illinois prairie. Through changes in M. pennsylvanicus numbers, predators had an indirect effect on P. leucopus spatial patterns and movements. Increased densities of Microtus following predator exclusion appear to have resulted in P. leucopus using smaller home ranges and ones in which there was relatively low Microtus activity. Predation risk may also be

responsible for a reduction in P. maniculatus movements. Future investigations should use factorial experiments in which predation and densities are manipulated simultaneously. This approach will help to increase our understanding of how predation risk and numerical fluctuation affect prey behavior.

CHAPTER 5

RESPONSE OF TWO LOW DENSITY PEROMYSCUS POPULATIONS TO INCREASED FOOD AVAILABILITY: A NATURAL AND MANIPULATIVE EXPERIMENT

Introduction

Experimental studies of population dynamics have generally fallen into one of two broad categories: (1) those focusing on the intrinsic biology of a species and (2) those focusing on extrinsic or biotic interactions (Krebs and Myers 1974, Lidicker 1994). The two categories are not mutually exclusive and both have met with success and failures. Population studies focusing on the extrinsic biology of a species can be approached from three levels: (1) food availability from the bottom-up; (2) interspecific competition within a trophic level; and (3) predation from the top-down. The most direct way to test for bottom-up effects is simply to provide additional nutrients or supplemental food, an approach utilized by numerous investigators (e.g., Newsome 1970, Licht 1974, Hansen and Batzli 1979, Taitt 1981, Taitt and Krebs 1981, Dijkstra et al. 1982, Berner and Grubb 1985, Wolff 1985c, Ostfeld 1986, Desrochers et al. 1988, Duquette and Millar 1995, Scheiger 1995). Boutin (1989) cited 62 such studies with small mammals. Supplemental feeding commonly increased the duration of the breeding season, adult body weight, decreased home range size,

and resulted in, on average, a two-fold increase in density. However, as Boutin (1989) points out, there is a need to relate responses to food supplementation to a variety of environmental conditions. The importance of disturbance has been recognized for 20 years (Horn 1975, Connell 1978). Disturbance, or periodic perturbations in the environment, can play a major role in determining the number of individuals in a population (Huston 1979, Reice 1994). Such disturbances often result in a substantial decrease in density. Yet most food supplementation studies have been carried out during periods of at least low-moderate densities of the target species. The reasons for this are obvious: locations with extremely few or no individuals provide little information on which to base a study.

In addition to the role of disturbance, it is generally accepted that both "bottom-up" and "top-down" forces are important in determining the dynamics of populations and the structure of communities (Leibold 1989, Matson and Hunter 1992, Power 1992, Strong 1992). Such forces have been well studied with invertebrates and in aquatic systems (Hunter and Price 1992, Power 1992), yet virtually ignored among terrestrial vertebrates (see Desy and Batzli 1989 and Krebs et al. 1995 for two exceptions). There are several reasons to suspect that a multifactorial experiment on top-down vs. bottom-up effects could prove fruitful in elucidating mechanisms controlling small mammal demography. Work with both invertebrates and in aquatic systems has shown that predation and food availability may interact to regulate population dynamics. The two-fold increase in small mammal food supplementation studies (Boutin 1989) that is often observed suggests another process, possibly

predation, is limiting populations. Also, it is unlikely that the complex small mammal population dynamics observed at mid-latitudes (e.g., Getz 1987) are the result of only single trophic level interactions. However, there is still continued debate as to whether multifactor approaches are useful for the study of vertebrate demography (Gaines et al. 1991, Lidicker 1991, Lidicker 1994). In order to address questions such as why food supplementation studies commonly result in only a two-fold increase in densities, and how predator switching behavior may regulate prey populations, simultaneous manipulation of food from the bottom-up and predators from the top-down is required. In addition, a knowledge of the predator behavior and ecology is essential. In this way, prey dynamics occurring at a local scale can be linked with predator foraging at a landscape scale.

Boutin's (1989) review illustrated the importance of scale when conducting food supplementation studies with vertebrates. Increased densities on the areas being manipulated may be the result of immigration. Any subsequent increase in productivity could result in a source habitat from which individuals disperse to surrounding areas (Pulliam 1988). Boutin (1989) recommended that the spatial scale of food supplementation experiments be increased. However, this is not always logistically feasible. An alternative approach is to use both "natural" and manipulative experiments. Natural experiments have the disadvantage that they are less rigorous than manipulative experiments, but the advantage that they can occur over much larger spatial scales (Diamond 1986). A combined approach can help to offset the inherent weaknesses of each design.

For this portion of the study, I addressed questions on the role of food availability in affecting demographic fluctuations of the white-footed mouse (Peromyscus leucopus). Trap records from October 1994 through May 1995 were used for analyzing population dynamics at the experimental site. Data from two of the alternative prey sites, both oak woodlots, was also used to compare demographic fluctuations of P. leucopus. One of the two woodlots underwent a high mast year; mast has been shown to be an important food source for P. leucopus (Ostfeld et al. 1996, Wolff 1996). Trap records from March 1994 through May 1995 were used for analyzing population dynamics in the woodlots. This permitted the following three questions to be addressed: following a severe disturbance and dramatic decline in numbers, does P. leucopus (1) increase numerically following the increased availability of naturally occurring food; (2) can any observed responses to changes in the natural food base be repeated using manipulative experiments; and (3) does predation from the top-down interact with food from the bottom-up to regulate small mammal densities?

Data Analysis

As in Chapter 3, small mammal demographic characteristics (i.e., density, survivorship, and weight) for each monthly census were summarized using the Capture-Mark-Recapture programs of Le Boulengé (1987). Trappability was calculated using Manly-Parr (Seber 1982) estimates. Densities were determined using minimum number known alive (MNKA) since the number of marked individuals

recaptured (Ri) commonly did not meet the assumptions of probability estimation techniques (Seber 1982, Pollock et al. 1990). The October 1994 through May 1995 data were used to test for "top-down" vs. "bottom-up" effects on Peromyscus leucopus demography. The following abbreviated codes were used for the four treatments: food not supplemented, predator present = -F, +P; food supplemented, predators present = +F, +P; food not supplemented, predator excluded = -F, -P; food supplemented, predator excluded = +F, -P. Trap records from March 1994 through May 1995 from the two oak woodlots were analyzed for the effects of mast availability on P. leucopus demography. A nonparametric Wilcoxon rank test was used for analysis of the acorn biomass data due to a strong positive skew (Zar 1984). The effects of predator exclusion on moderate to relatively high densities of P. leucopus, along with P. maniculatus and Microtus pennsylvanicus, have been discussed previously (Chapter 3).

For the continuous response variables (i.e., density and weight), regression lines were fitted to the data and F-values calculated to see if higher order polynomials added significant explanatory strength to the models. The best fit models were then tested for autocorrelation using the Durbin-Watson statistic (Ostrom 1990) produced by SAS PROCEDURE REG (1990a). Since the time series were relatively short, significant autocorrelation was not a problem and treatment effects were tested with a covariate analysis using SAS PROCEDURE GLM (SAS 1990a). Canid activity at the predator access-food supplemented and predator access-unsupplemented plots was analyzed using a one-way repeated measure ANOVA with SAS PROCEDURE GLM

(SAS 1990a). Inference was based on Huynh-Feldt adjusted P-values (Huynh and Feldt 1976). For all parametric analyses, residuals were inspected for departures from normality using box-plots and normal probability plots (Tukey 1977) and inferences based on type III sums-of-squares. The biomass of acorns in both oak woodlots was highly skewed. Consequently, nonparametric Wilcoxon rank-sum scores were used to test for a significant difference. All analyses were considered significant at $\alpha = 0.05$. The data are presented graphically for all significant values appearing in the ANOVA tables and those that are close to significant and/or have ecologically meaningful trends.

Survival analyses were conducted using the log-rank test of SAS PROCEDURE LIFETEST (SAS 1990a). Statistical comparisons of overall survival were conducted with the nonparametric log-rank test, which is robust to differences in survival curve shape and does not assume any particular underlying distribution (Fox 1993, Lee 1980). Two pre-planned comparisons, food supplemented-predator access vs. food supplemented-predator exclusion and food supplemented-predator access vs. not supplemented-predator access, were conducted.

Results

Subsequent to the severe ice storm in January 1995, densities of P. leucopus declined dramatically (Fig. 6). Sampling at the six alternative prey locations showed the effect was not restricted to the experimental site, but was widespread over several thousand hectares (Chapter 3; Fig. 5). At two of these sites, the oak woodlots, P.

leucopus densities were similar between March and August 1994 (Fig. 20). However, following high production, acorn biomass on the forest floor was 17 times greater in oak Woodlot I as compared to oak Woodlot II (Fig. 21), a highly significant difference ($S = 3225.00$, $Z = 4.032$, $P = 0.001$). Acorns began dropping in August, which was followed by a dramatic increase in P. leucopus numbers. Acorns ceased dropping in approximately mid-October, with mouse numbers reaching their peak in November. Following the peak, P. leucopus declined dramatically, with the number of individuals recorded in January being similar to pre-mast abundance; numbers remained relatively stable following the decline. In oak Woodlot II, mouse abundance remained relatively stable during the time period of large fluctuations in Woodlot I.

The ANCOVA showed that the change in P. leucopus numbers over time was highly significant and that the change occurred as a quadratic response (Table 26). Overall, numbers were also significantly greater in Woodlot I as compared to Woodlot II. Of particular importance are the two highly significant interaction terms, Time and $Time^2$ crossed with Woods (Table 26). The interactions show that the number of Peromyscus significantly diverged and then subsequently converged.

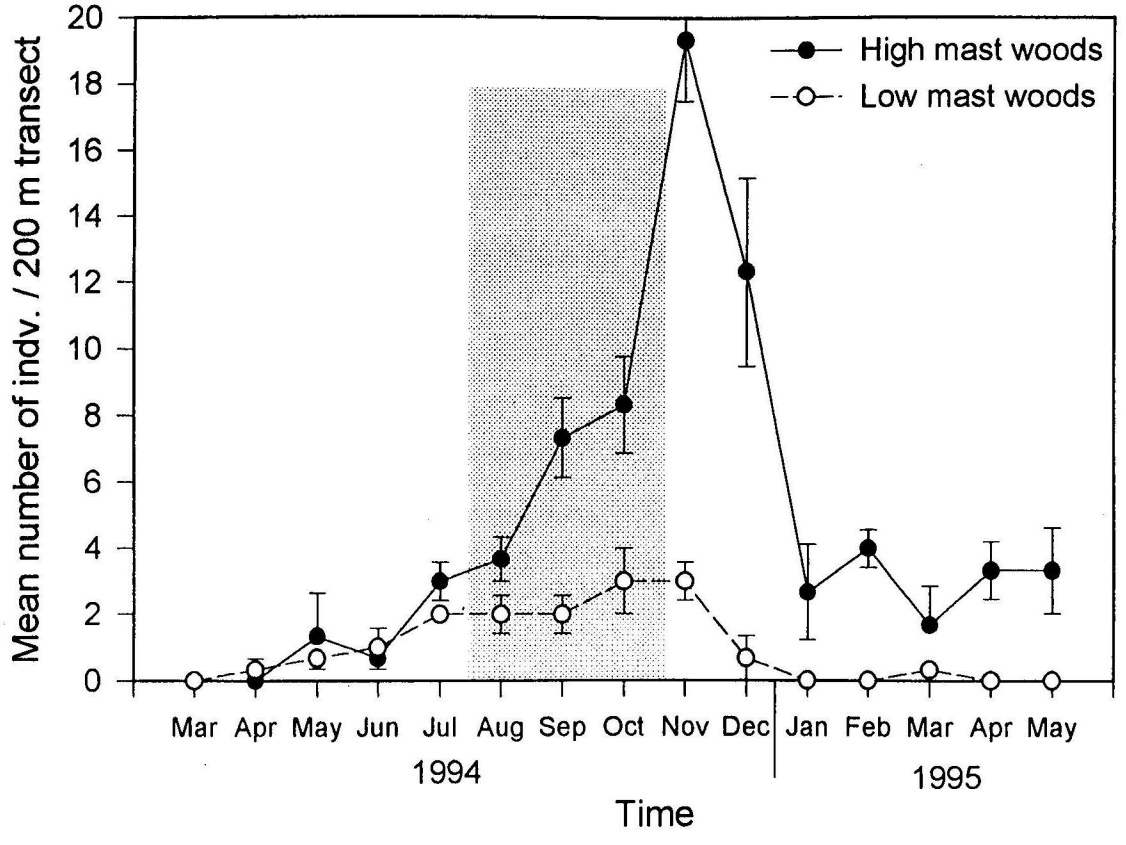

Figure 20. Population dynamics of P. leucopus in oak woodlots with high and low mast production. The stippling indicates the period when acorns were dropping.

Figure 21. Acorn biomass in the two oak woodlots.

Table 26.

Analysis of covariance table of Peromyscus leucopus densities in high mast vs. low mast oak woods

Source	df	MS	F	P
Woods	1	53.217	5.24	0.025
Time	1	350.512	34.52	0.001
$Time^2$	1	324.023	31.91	0.001
Time x Woods	1	145.827	14.36	0.001
$Time^2$ x Woods	1	112.944	11.12	0.001
Error	84	10.153		

Following the initial increase in P. leucopus densities in Woodlot I is when food supplementation was initiated at the experimental site (October 1994). All four treatments (-F, +P; +F, +P; -F, -P; +F, -P) had an increase in numbers between October and December, a seasonal pattern commonly observed among Peromyscus in the Midwest (Baker 1983, Hoffmeister 1989). There was a decrease in numbers during January, a trend also observed at the six alternative prey sites (Fig. 5). The decrease was probably due to extremely low trap success as a result of several days of

continued snow. Previous work has shown that recent, moderate snowfall can substantially reduce the number of individuals captured (personal observation). For the duration of the supplementation experiment the number of individuals on the -F, +P and -F,-P plots remained relatively constant. However, by February, there was an approximately three-fold increase in densities on the food supplemented plots as compared to the unsupplemented plots (Fig. 22). Subsequent to the increase, numbers declined steadily until densities converged on the supplemented vs. unsupplemented plots in May.

Overall, densities were significantly greater on the +F plots as compared to the -F plots and the number of individuals changed significantly over time in a quadratic fashion (Table 27). Both the Time x Food and Time^2 x Food interactions were highly significant, reflecting the strong increase and subsequent decrease in the number of Peromyscus on the food supplemented plots (Fig. 22). There was also a Predator x Food interaction, which was the only indication of a predator exclusion effect on P. leucopus. Means of the four treatments were collapsed over time in order to construct an interaction plot and illustrate the direction of the effect. Overall, densities were lowest on the -F, +P plots, intermediate on the +F,+P and -F, -P plots, and highest on the +F, +P plots.

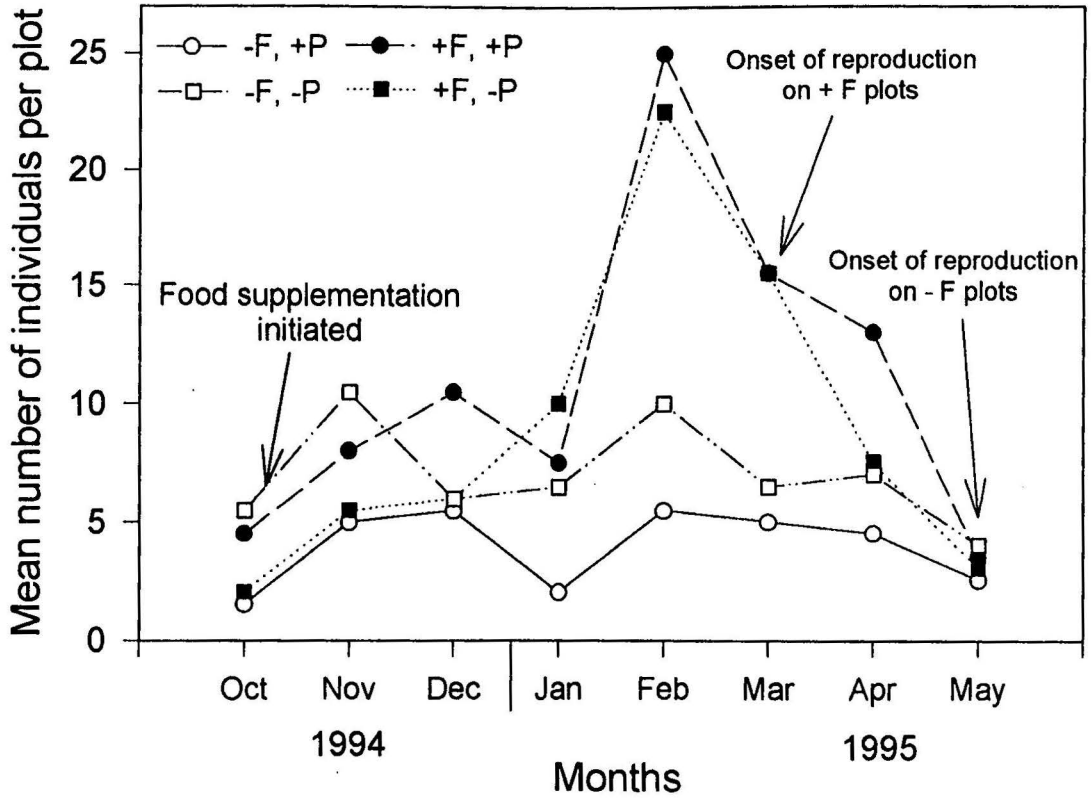

Figure 22. Population dynamics of P. leucopus on control, food supplemented, predator excluded, and food supplemented + predator excluded plots.

Table 27

Analysis of covariance of Peromyscus leucopus densities on predator exclusion vs. predator access and food supplemented vs. unsupplemented plots

Source	df	MS	F	P
Predation	1	0.001	0.01	0.996
Food	1	133.683	5.09	0.028
Time	1	545.615	20.77	0.001
$Time^2$	1	526.251	20.03	0.001
Pred x Food	1	107.640	4.10	0.048
Time x Pred	1	1.537	0.06	0.810
Time x Food	1	274.216	10.44	0.002
$Time^2$ x Pred	1	2.768	0.11	0.747
$Time^2$ x Food	1	242.590	9.23	0.004
Error	54	26.274		

The significant increase in Peromyscus densities on the food supplemented plots during mid-winter attracted canids to the +F, +P plots (Fig. 23). This resulted in a significant Activity effect, a marginally significant Time effect, and, in particular, a Time x Activity interaction (Table 28). As Peromyscus, or prey densities decreased on the +F plots so did canid activity (i.e., the significant interaction). Thus, within a habitat, predators were able to "cue-in" on abundant patches of food.

At the onset of reproduction, there was no significant difference in the mean proportion of reproductively active females on the four supplemented (51%±1.75SE) versus the four unsupplemented plots (58%±4.62SE) ($t = 1.265$, $df = 6$, $P = 0.252$). However, the onset of reproduction on the supplemented plots occurred in March, two months earlier than the unsupplemented plots (Fig. 22). The small sample size in Woodlot II precluded an inter-woodlot comparison of P. leucopus reproduction. However, there was no particularly notable increase in either the proportion of reproductively active females or juvenile recruitment in Woodlot I. On the contrary, reproduction ceased in November, which is the same as P. leucopus at the experimental site in the years proceeding, during, and following the mast response. Finally, juveniles accounted for 9%, 16%, 10%, and 2% of the individuals during September-December, respectively. Juvenile recruitment at the experimental site was either similar to or higher during these months in the years proceeding, during, and following the mast response. Consequently, it is unlikely that recruitment was responsible for the numerical increase of mice following mast production.

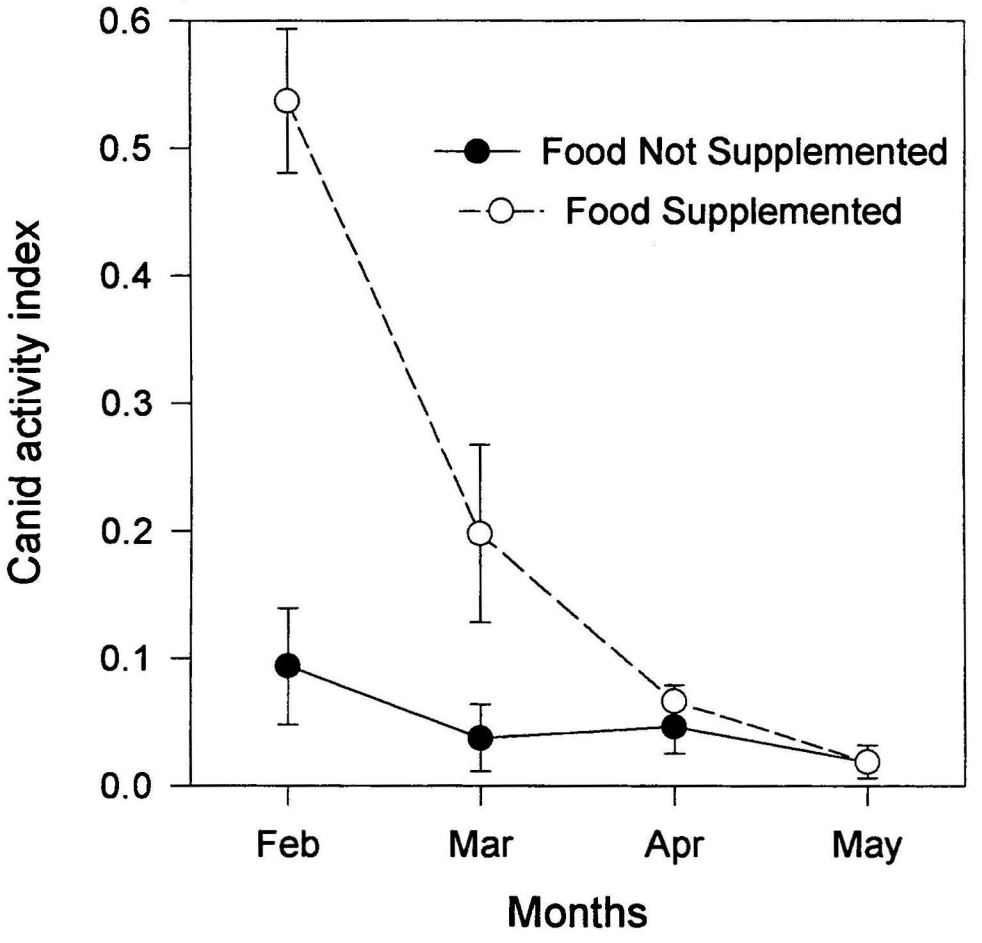

Figure 23. Coyote activity adjacent to predator access plots that had food supplemented (high to low Peromyscus densities) and unsupplemented (low Peromyscus densities).

Table 28

Repeated measures analysis of variance table for canid activity around the food supplemented vs. unupplemented 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		

There was no significant difference in survivorship between the two woodlots (Fig. 24a) ($\chi^2 = 0.045$, df = 1, P = 0.831). Similarly, there was no overall significant difference in survivorship between the -F +P, +F +P, -F -P, +F -P plots (Fig. 24b) ($\chi^2 = 1.348$, df = 3, P = 0.718). Mean survivorship (in days) on the four treatments was: -F +P = 41.03; +F +P = 30.77; -F -P = 38.10; +F -P = 40.72, with the maximum ranging from 157 to 186 days. The lack an overall predator exclusion effect on P. leucopus densities was corroborated by one of the planned survival comparisons: there

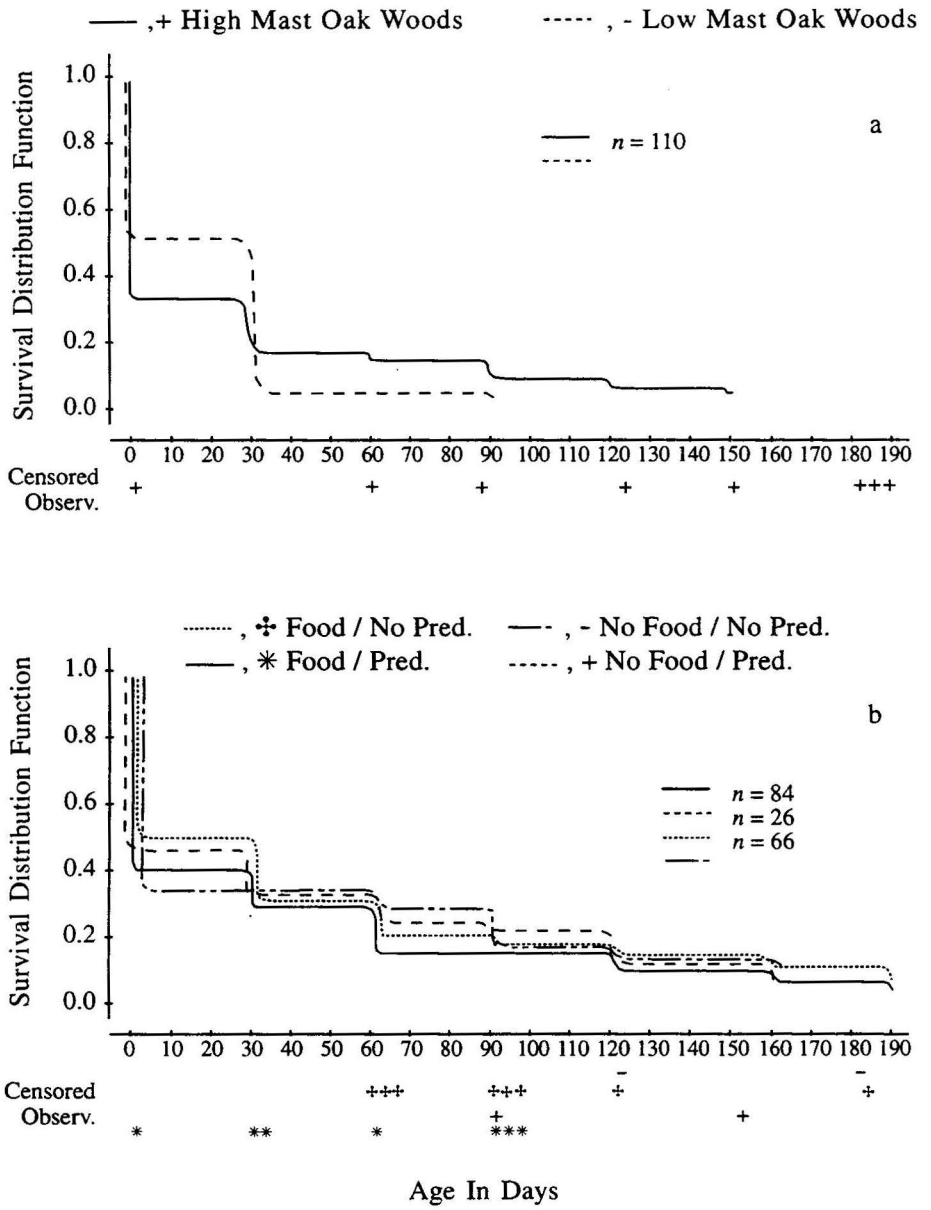

Figure 24. Survival distribution function, the probability of an individual age *t* having a lifetime exceeding *t*, for Peromyscus leucopus. Below the abcissa, each symbol for a censored observation (i.e., right censored) represents an individual captured at the last trap session and its fate unknown. (a) Survivorship in a high and low mast oak woodlots. (b) Survivorship for the top-down vs. bottom-up experiment.

was no significant difference between survivorship on the +F -P and +F +P plots (χ^2 = 1.091, df = 1, P = 0.296). There was, however, a significant difference for the second planned comparison (χ^2 = 6.386, df = 1, P = 0.012); survivorship was significantly greater on the -F +P plots as compared to the +F +P plots.

There was a marginally significant effect of increased mast availability on P. leucopus body weight (Table 29). On average, individuals tended to weigh more in the low mast woods (Fig. 25). Due to relatively small sample sizes, the beginning (April-July) and end (March-May) of the time series should be interpreted with caution. During the central portion of the time series, body weights between the two woodlots fluctuated similarly. However, contrary to usual predictions, body weights were greater in the area with lower food availability. A possible explanation is increased competition for food as a result of the strong numerical response to the large mast crop. This is at least partially corroborated by the rapid decrease in mean weight between October and November in the high mast woodlot, the duration when the number of individuals increased at the greatest rate (ca. 2.5-fold in one month). Peromyscus leucopus body weights fluctuated significantly during the course of the food supplementation experiment (Table 30, Fig. 26). Overall, body weights declined between October and December, and subsequently increased slightly through March. Between March and April mean body weight increased substantially. The significant quadratic term (Time^2) is a result of the overall decrease and subsequent increase in mean body weight. At the experimental site, there was a significant overall effect of food supplementation. Mean body weight tended to be somewhat greater as a result

Table 29

Analysis of covariance of mean Peromyscus leucopus body weights in a high mast oak woods vs. a low mast oak woods

Source	df	MS	F	P
Woods	1	31.207	3.13	0.083
Time	1	0.048	0.01	0.945
Error	47	9.983		

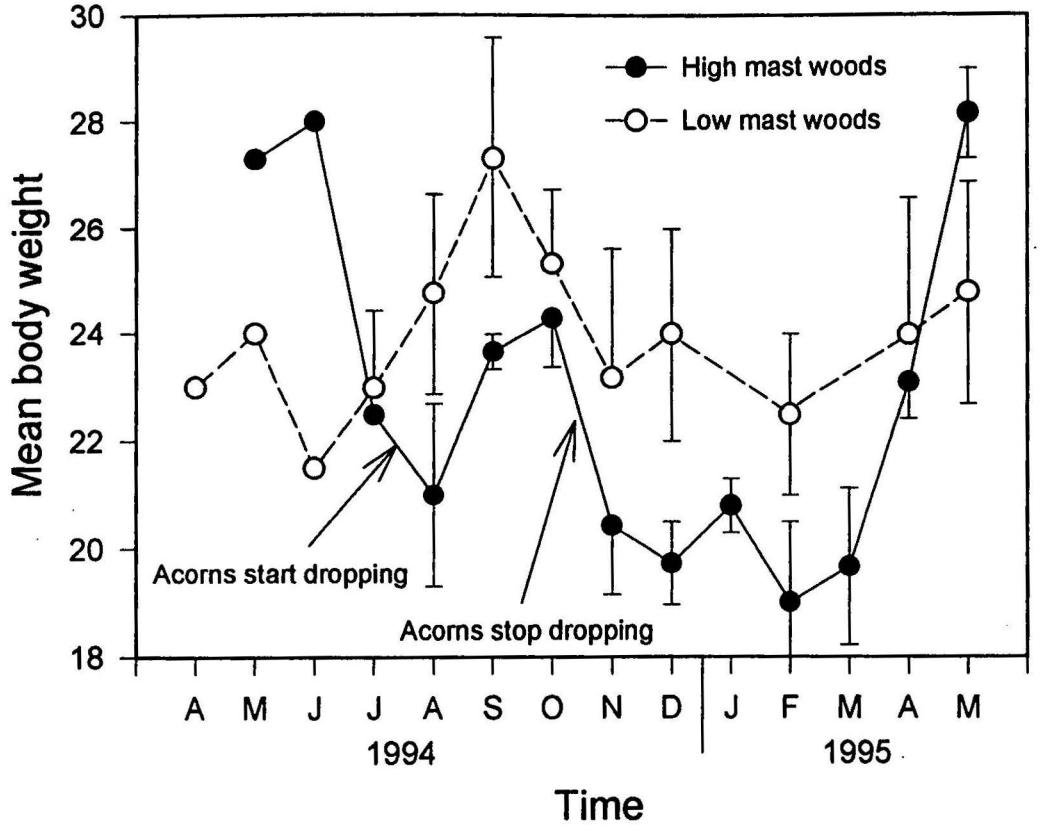

Figure 25. Mean body weights of P. leucopus in oak woodlots with high and low mast production.

Table 30

Analysis of covariance of Peromyscus leucopus body weights on predator exclusion vs. predator access and food supplemented vs. unsupplemented plots

Source	df	MS	F	P
Predation	1	2.861	0.74	0.395
Food	1	18.098	4.66	0.036
Time	1	41.146	10.58	0.002
$Time^2$	1	81.891	21.06	0.001
Pred x Food	1	18.473	4.75	0.034
Pred x Time	1	0.115	0.03	0.864
Food x Time	1	19.478	5.01	0.029
Pred x $Time^2$	1	0.235	0.06	0.817
Food x $Time^2$	1	15.955	4.10	0.048
Error	48	3.887		

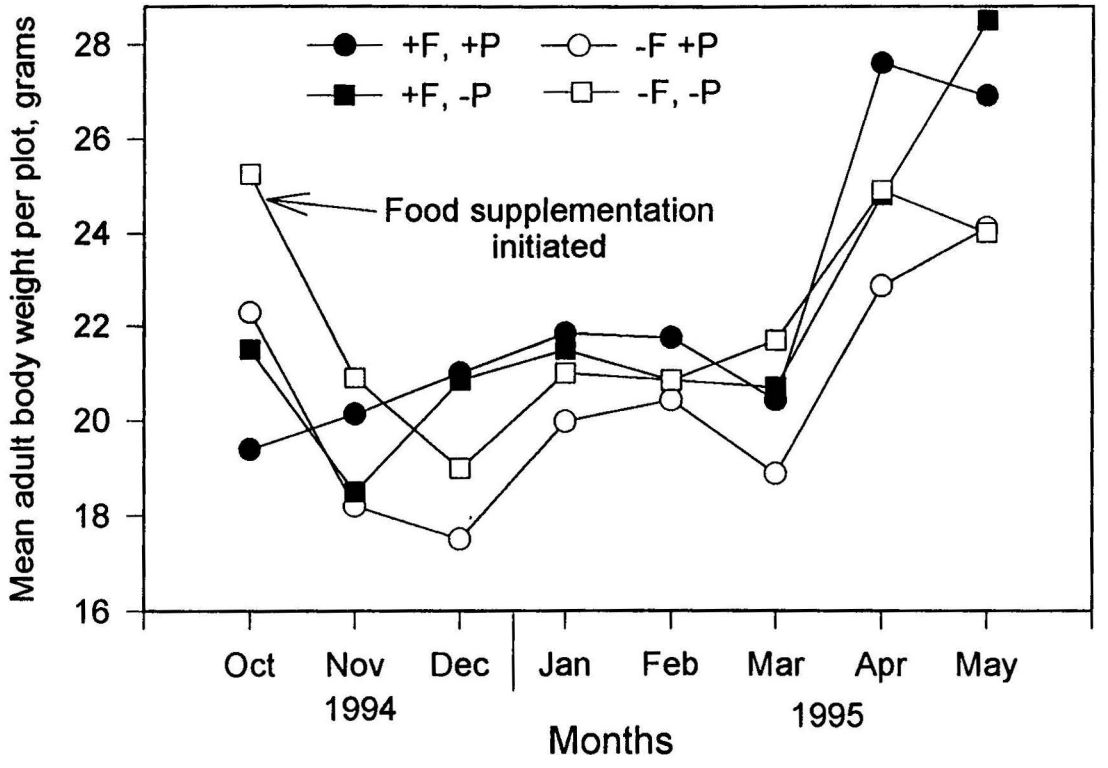

Figure 26. Mean body weights of P. leucopus on control, food supplemented, predator excluded, and food supplemented + predator excluded plots.

of increased food availability (Fig. 26). There were also significant Food x Time and Food x Time^2 interactions; body weight increased at a greater rate on the supplemented vs. unsupplemented plots, particularly between March and May. Food supplementation and predator exclusion resulted in a significant interaction for body weight.

Discussion

In January of 1995 a severe ice storm resulted in a drastic decline in Peromyscus numbers at the experimental site and six alternative prey sites. By late summer populations had still not approached pre-ice storm abundance. There was no reason to suspect populations were limited by food, as precipitation and, presumably, plant productivity were about average. Also, at the experimental site, there was no indication of a numerical effect resulting from predator exclusion. One possible explanation for the absence of a numerical increase in P. leucopus density in 1995 is the Allee effect (Allee 1938). Under extremely low density conditions, dispersion of individuals across the landscape reduces their likelihood of finding mates.

However, in the late summer of 1995, P. leucopus populations increased dramatically as a result of high mast production on a 6.2-ha woodlot. There was no indication that increased recruitment, in situ or otherwise, was responsible for the numerical response. This leaves immigration as the best explanation. Even though there was probably an adequate food supply for Peromyscus that were highly dispersed across the landscape, individuals still "cued-in" on and responded to a

particularly abundant patch of food. As emphasized, the abundance of mice across the landscape was very low, including oak Woodlot I prior to mast production. Thus there was no social fence (sensu Hestbeck 1982, 1988) to preclude rapid immigration and the subsequent increase in numbers. What is unclear, is why there was not a significant increase in reproduction, expressed as either the percent reproductively active females or extending further into the breeding season. Such changes in reproduction have been observed previously following high mast years (Ostfeld et al. 1996, Wolff 1996). The only difference between this and the previous two studies is the extremely low densities as a result of the large scale disturbance. A somewhat speculative explanation is that the low probability of encountering mates resulted in a relatively low proportion of individuals entering into reproductive status.

The pattern of numerical increase at the experimental site was similar to that observed for the woodlot. No reproductively active individuals were recorded in November; this was also the last month juveniles were observed until the following spring. Consequently, the numerical response may again be attributed to immigration. The main difference was that the response at the experimental site was substantially more protracted. Two explanations may account for the difference. First, the January trap census may not have accurately portrayed the true densities. There was a noticeable drop in the number of individuals captured on all four treatments. A similar decrease in the number of individuals, as compared to December and February, was observed at several other locations at Fermilab. The decreased number of captures was accompanied by moderate, regular snowfall, which can reduce the trap success of

P. leucopus (personal observation). Although the reduced trap success probability contributed to the protracted response (i.e., in the month of January, not any of the proceeding months), a more likely and robust explanation is the area receiving supplemental food. The comparatively large size of the woodlot (6.2 ha) substantially increased the probability of individuals locating the abundant food source, as compared to the 0.6-ha manipulative plots. This is one of the principal advantages of natural experiments, that is, their relatively large size. An advantage of the manipulative experiment is that it was possible to maintain the increased food availability into the spring. Following the peak in February, P. leucopus numbers declined steadily until densities on the supplemented and unsupplemented plots converged in May. Accompanying the decrease in numbers on the food supplementation plots was the earlier onset of reproductive activity, occurring two months before the unsupplemented plots. It has been shown that P. leucopus uses group nesting during winter months to help thermoregulate (Vogt and Lynch 1982, Madison et al. 1984). This requires that individuals not defended territories. Alternatively, Ostfeld (1985, 1990) has shown theoretically that female small mammals establish territories to defend patchily distributed food. Pregnant and lactating females have high energy demands and the defense of an abundant food source can aid in the necessary procurement of energy. Several studies support Ostfeld's model (see Ostfeld 1985, 1990 and citations therein), including work with Peromyscus (Wolff 1989). Consequently, I would suggest that the ultimate reason that individuals were able to immigrate at a rapid rate onto the supplemented plots was not only low

densities, but also the absence of territorial defense. With the onset of reproduction, individuals began to reestablish territories. This led to the exclusion of conspecifics and the observed decrease in density. An analysis of capture points supports this conclusion. During December through February, individuals showed a significantly clumped distribution on the food supplemented plots. During July through August, 1995, a period of active reproduction, individuals were more evenly distributed with a mean weighted overlap of only 17% on the control plots

Boutin (1989) has suggested that the reason small mammal food supplementation studies have, on average, only demonstrated a two-fold increase in densities is increased predation intensity. Ford and Pitelka (1984) even coined a special term for the predator response: "the pantry effect." The pantry effect assumes predators "cue-in" on an abundant patch of prey, much the same as the small mammals immigrating into abundant patches of food. The increased predator foraging subsequently limits prey densities. Factorial experiments can be used to test for predator limitation of prey increasing as a result of food supplementation. However, only two such experiments have been carried out with vertebrates (Desy and Batzli 1989, Krebs et al. 1995). Desy and Batzli (1989) and Desy et al. (1990) studied seeded populations of prairie voles (M. ochrogaster) in a central Illinois bluegrass field using an impermeable design with dispersal sinks. A 2 x 2 factorial design of food supplementation and predator exclusion was used on replicated 0.13-ha plots. The experiment was repeated over three years, each time for a duration of either 12 or 24 weeks. The investigators detected a significant increase in vole densities and survival on predator excluded

plots; food supplemented plots showed a significant increase in density. The results of the interaction indicated additive and equal effects on density. That is, both biotic interactions were significant and of relatively equal importance. Food supplementation and predator exclusion also resulted in a significant interaction for body growth rates and adult body size. The significant interaction was attributed to predators inhibiting the growth response to supplemental food, as a result of more restricted movements. Working in the Yukon, Krebs et al. (1995) investigated top-down and bottom-up effects on snowshoe hares (L. americanus). Mammalian predators were excluded from two 1-km^2 areas using electric fencing. Supplemental food (rabbit chow) was spread ad lib across one of the two enclosures and a third 1-km^2 area to which predator had access. The experiment was effective as of January 1989. The supplemental food resulted in 1.5- to 6-fold increases in densities as compared to a control. The numerical response to predator exclusion was similar (1.4- to 6-fold). When averaged over the duration of the study, the food supplementation + predator exclusion treatment resulted in an 11-fold increase in density. During the late decline phase, L. americanus densities were 36 times greater on the interaction plot as compared with the control. Thus, food and predation interacted multiplicatively to determine L. americanus densities.

Contrary to the two previous studies, food availability and predation had neither additive nor multiplicative effects on P. leucopus densities. Rather, densities were the highest on +F, +P plots, lowest on -F, +P plots, and intermediate on the +F, -P and -F, -P plots. The pantry effect may explain the observed responses, although not in the

manner usually expected (i.e., densities greatest on +F, -P treatments). If the increase in densities on the +F plots was the result of immigration, and predators removed a substantial portion of these individuals as they entered the population, a rapid turnover would result in a greater number of individuals being captured over time. Two lines of evidence support this conclusion. First, there is the pattern of canid foraging. When Peromyscus densities were at their highest on the +F, +P plots in February, so was canid activity; activity declined in relation to a decrease in prey. Over the same period of time, canid activity and prey densities remained relatively constant on the -F, +P plots. Specifically, predators "cued-in" on the abundant food source. Second, there is the significantly greater survivorship on the -F, +P as compared to the +F, +P plots. This is contrary to usual prediction that an increase in food availability will result in increased survivorship. However, it does support the idea that an increase in predator foraging resulted in a rapid turn-over of individuals and the significant Predator x Food interaction.

In conclusion, very low densities of P. leucopus responded numerically to increased food availability. Results for a relatively large "natural" experiment and a more controlled manipulative experiment were similar. In both cases, the increase in numbers was due primarily to immigration, not reproduction. The natural experiment showed a more rapid numerical increase, presumably due to its larger spatial scale. Increased food availability in the spring resulted in an early start in reproduction, and, probably, a decline in numbers due to territorial defense. The food supplementation

led to increased predator activity and decreased survivorship of the prey. This resulted in a rapid turnover of individuals and a significant Predator x Food interaction.

CHAPTER 6

GENERAL SUMMARY

The review in Chapter 1 demonstrates that numerous intrinsic processes and biotic and abiotic interactions may play a role in determining small mammal demography. The relative importance of these different interactions can vary widely, both within and between taxonomic groups as shown by the results of this and numerous other studies. One possible exception is disturbance, whose effects appear to be pervasive, not only among most taxonomic groups, but also across a variety of ecological systems. Responses to disturbance can be either positive or negative. In several habitats, fire can result in both a substantial increase and decrease in small mammal numbers; the direction of the response depends upon the species. ENSOs may elicit strong numerical responses of an entire small mammal assemblage, but in a heterogenous manner. Severe ice storms can cause dramatic declines in the numbers of small mammals, as was shown in this study.

Differences in the biology of a species largely determine the magnitude of response to a disturbance. For example, although Peromyscus declined dramatically as a result of the ice storm, there were clearly a few individuals across the landscape which survived. Similar to Peromyscus, the number of Microtus decreased dramatically as a result of the storm; however, the effect on Microtus was more

pronounced since even fewer individuals survived as compared to Peromyscus. The difference between the two genera may be partially attributed to variation in habitat utilization. At Fermilab, P. leucopus is common in a variety of different habitats, including tallgrass prairie, shrubby oldfields, savanna, and woodlots. In addition, both P. leucopus and P. maniculatus may use a variety of different nest sites: under logs, tree holes, burrows of larger mammals, rocky crevices and cracks, and elevated grass nests constructed in dense shrubs and grasses. Several of these locations, particularly tree holes and rocky areas, provide shelter from storms. Alternatively, Microtus, and particularly M. pennsylvanicus, is generally associated with grassland habitats. Since grasslands are relatively open and have little or no woody material, there are few microhabitats providing shelter from severe weather. Also in contrast to P. leucopus and P. maniculatus, M. pennsylvanicus either nests at or just below the surface of the ground, affording little or no protection from thick layers of ice. Consequently, Microtus populations are very susceptible to severe weather, which may cause dramatic declines such as observed in this study.

Recovery of Microtus populations in grasslands may be protracted due to limited dispersal between habitats. For example, P. leucopus can have individuals survive an ice storm in protected microhabitats of a woodlot. Following a storm, individuals can then disperse from the woodlot to a prairie. Microtus are less likely to have such "founder" populations to recolonize or increase the number of individuals in a location where densities have crashed. However, relatively low rates of inter-habitat movements may also partially explain the rapid increase in Microtus densities

sometimes observed. For species that regularly move between habitats, one location may act as a sink (sensu Pulliam 1988), regulating a source population. Between P. leucopus and M. pennsylvanicus it is interesting to note that the former, a habitat generalist, showed greater population stability than M. pennsylvanicus during the course of this investigation.

By their very nature, disturbances only occur periodically. In between disturbance intervals, which can be periods of several years, both intrinsic and extrinsic processes may determine small mammal population dynamics. The two small mammal genera which have received the greatest amount of attention in this respect are Peromyscus and Microtus. Intrinsic or social regulation may play the predominate role in determining Peromyscus numbers between disturbance events. This study clearly demonstrated that predators do not limit densities of either P. leucopus or P. maniculatus. An increase in food availability resulted in increased P. leucopus densities, but this appeared to occur primarily during the nonbreeding season. When individuals are reproductively active, there is evidence that territorial defense may limit densities, even when there are abundant patches of food. The one exception to this may be when abundant food resources are widely distributed across a large spatial scale, such as high mast production in extensive tracts of oak forest. This may also explain why most of the food supplementation studies summarized in Table 2 only showed a maximum two-fold increase in densities and the results of the top-down vs. bottom-up experiment in this study were neither additive nor multiplicative. Also, for a habitat generalist, subordinate individuals that do not obtain a territory may readily

disperse to another location. Thus, it can been seen how relatively structured social systems that include territorial defense, along with habitat generalists in a relatively heterogeneous environment, can lead to stable population dynamics.

Interspecific competition may be the one biotic interaction important in determining Peromyscus population dynamics. Several studies reviewed in Chapter 1 demonstrated asymmetrical competition between microtines and other small mammals. These investigations found that Microtus reduced and even excluded populations of Peromyscus, Reithrodontomys, and Mus. In this study, a numerical response by Microtus to vertebrate predator exclusion provided the opportunity to examine Peromyscus-Microtus competition in tallgrass prairie. At both moderate, and even relatively low voles densities, there was a inverse correlation between P. leucopus and M. pennsylvanicus. Particularly interesting is that variation in M. pennsylvanicus densities attributed to predation can significantly influence P. leucopus abundance. Since there is a relatively low degree of dietary overlap between the two species, it is unlikely that they are competing for food. Instead, M. pennsylvanicus appears to reduce spatial movements of P. leucopus. This results in decreased home range size and increased home range overlaps of the latter species.

Although intrinsic regulation probably plays a role in determining Microtus densities, I would suggest that biotic interactions are of greater importance. This is illustrated by the effect that predator exclusion had on M. pennsylvanicus densities. During two years, following annual peaks in densities, predators significantly depressed the number of M. pennsylvanicus. The two other predator exclusion studies

carried out with Microtus corroborate these results. However, this is the only study to simultaneously monitor alternative prey at numerous locations across the landscape, document predator diet selection in relation to prey abundance, and relate results of the predator foraging to experimentally manipulated prey dynamics at a meso-scale. Results of the investigation provide support for Erlinge et al.'s (1983, 1988) model: in a heterogeneous landscape, generalist vertebrate predators can select alternative prey populations, in turn depressing relatively abundant populations of preferentially selected prey.

The food supplementation studies summarized in Table 1 provide additional support that biotic interactions play an important role in determining Microtus population dynamics. A majority of these studies found a greater than two-fold increase in densities as a result of food augmentation. This study provides support that food availability in tallgrass prairie may limit Microtus densities, albeit seasonal. Although there was a significantly greater number of voles on the predator exclusion plots, the number of individuals still declined in the fall. During the two years when moderate numbers of voles were present at the site, the fall declines began shortly after the first heavy frost. The frost kills the above-ground portion of prairie vegetation and, presumably, results in a substantial reduction in the Microtus food base. The conclusion that food, along with predation, is important in determining Microtus densities during years between disturbance events, was corroborated by necropsy of individuals found dead at the site. The vast majority of such individuals had little or no

food in the their stomachs. Future work should include "top-down" vs. "bottom-up" experiments on naturally fluctuating populations of microtines.

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