

The Ecological Effects of Carnivores on Small Mammals and Seed Predation in
the Albany Pine Bush

Abstract of
a thesis presented to the Faculty
of the University at Albany, State University of New York
in partial fulfillment of the requirements
for the degree of
Master of Sciences
College of Arts & Sciences
Department of Biology
Program in Biodiversity , Conservation & Policy

Amielle A. DeWan
2002

Abstract

Habitat fragmentation can alter ecological processes by modifying species composition, population sizes, and key ecological interactions, although evidence for the latter is scarce. The immediate effects of fragmentation can be magnified by edge effects in the habitat that remains. The objective of this study was to examine how habitat fragmentation and edge effects can influence small mammal and native plant communities, through carnivore-mediated trophic cascades. This research was conducted in the Albany Pine Bush, a globally rare ecosystem that has become highly fragmented by urbanization. I experimentally evaluated small mammal abundance and seed predation rates on three native plants species at three site types: small fragments (<12ha), interiors of large fragments (>40ha) and edges of large fragments. Seeds of pitch pine (*Pinus rigida*), blue lupine (*Lupinus perennis*) and New Jersey tea (*Ceanothus americanus*) were chosen because of their conservation importance, and because natural populations have suffered historic declines. Track tube surveys, a new method for recording small mammal activity, were conducted at each of 21 sites in summer to determine relative abundance, using standard baits. Surveys were repeated in fall using native seeds as bait to determine relative seed predation rates. Data on carnivore activity for each site were drawn from a separate, ongoing study by researchers at the New York State Museum (R. Kays, D. Bogan). Seven small mammal species were found during summer surveys, three of them restricted to large fragments (*Tamiasciurus hudsonicus*, *Glaucomys sabrinus* and *Napeozapus insignis*). However, only three widespread and abundant small mammals accounted for the overwhelming majority of native seed removal (*Peromyscus leucopus/maniculatus*, *Sciurus carolinensis* and *Tamias striatus*), and of these 72% of all seeds were removed by *P. leucopus/maniculatus*. Relative abundance of small mammals did not appear to vary in relation to site type. However, seed predation rates were highest at the edge of large fragments.

The increasing presence of coyotes (*Canis latrans*) in the Albany Pine Bush has been implicated in modified trophic interactions, due to their potential to reduce populations of smaller predators, thus releasing small mammals from some forms of predation pressure. However, a direct relationship linking carnivores, small mammal abundance and seed predation was not clear. The results of my study do suggest that seed predation may play an important role in the regeneration of key plant species, and preserve managers should consider the role of small mammals when planning restoration efforts. Longer-term studies are needed to better understand the influence of top-predators on the small mammal and plant community in fragmented landscapes.

Acknowledgements

I would like to thank the chair of my committee, Dr. George Robinson, for all of his guidance and support. Dr. Robinson has been an exceptional mentor through his commitment to this project and to the Biodiversity program. I would like to thank my committee members Dr. Charles Smith and Dr. Roland Kays. I would like to thank the Albany Pine Bush Commission for allowing me to conduct research in the preserve. I especially want to thank Daniel Bogan and the New York State Museum for providing data and funding. Additionally, I would like to thank Jared Wagner for his assistance in the field. Finally, I would like to thank my family for all of their love and support.

Abstract	ii
Acknowledgements	iv
List of Tables	vii
List of Figures	viii
1 Introduction	1
1.1 Habitat fragmentation and species interactions	1
1.2 Trophic Cascades and Habitat Alteration	3
1.3 Influence of Seed predation on Plant Communities	6
1.4 Habitat Fragmentation and Trophic Responses in the Albany Pine Bush	7
1.4.1 Fragmented state of the Albany Pine Bush	7
1.4.2 Putative Food Webs in the Albany Pine Bush	8
1.5 Objectives	11
2 Methods	16
2.1 Study Sites	16
2.2 Characterization of the Small Mammal Community	18
<u>2.3</u> Seed Predation Experiments	21
<u>2.4</u> Carnivore Monitoring	22
<u>2.5</u> Analytical Methods	25
3 Results	31
3.1 Species-Area Relationship	31
3.2 Small Mammal Abundance	31
3.3 Species Ordinations and Treatments	32
3.4 Seed Predation	33
3.4.1 Seed Preference	33
3.4.2 Seed predation and edge effects	33
3.4.3 Small Mammal Occupancy and Seed Predation	34
3.5 Canonical Correspondence Analysis	34
4 Discussion	56
4.1 Species-Area relationships	56
4.2 The small mammal community	57
4.3 Higher trophic interactions	59
4.4 Seed Predation	60

4.4.1	Seed Preferences	60
4.4.2	Seed predation and edge effects	61
4.4.3	Small Mammal Occupancy and Seed Predation	61
4.5	Trophic Interactions: Missing Links	62
5.	Conclusions	65
	Literature Cited	66
	Appendices	71

1 Introduction

1.1 Habitat fragmentation and species interactions

Human activities such as agriculture, forestry and suburban development continue to reduce and fragment much of our natural landscape. Habitat fragmentation reduces the size of natural patches, increases the ratio of edge to interior in patches and increases the distance between patches. In addition, the effects of fragmentation can be magnified by edge effects in the habitat that remains (reviewed by Lindenmayer et al. 1999). These factors can affect the structure and function of ecological communities by changing species composition and by modifying key ecological interactions.

Forest fragmentation reduces the total area and alters the landscape matrix of remaining habitat patches. Organisms that remain in these patches are then exposed to a different surrounding habitat types and their responses to this change have been termed 'edge effects' (Murcia 1995). Edge effects are usually described as the community or population response to discontinuities or boundaries between habitat types (Lidicker 1999). The increase in the ratio of edge to interior can increase edge effects in remaining habitat patches and can have a variety of consequences. Edge effects mediated through physical and chemical environment can directly affect the distribution of species near the edge (Murcia 1995). Forest animal species in particular have shown diverse ecological responses to edge effects (reviewed by Murcia 1995), which can also indirectly affect mortality and reproduction through increased pressure from predators, competitors, parasites and disease (Krebs 1994). For example, it has been shown that in many locations, rates of predation on avian nests are higher at or near habitat edges associated with forest fragmentation (reviewed by Bayne & Hobson 1998).

Although the response of predators to fragmentation may be affected by multiple landscape features (Oehler & Litvaitis 1996), increased predation has been attributed to the response of predators to a greater density of prey associated with habitat edges. However, mammals can show diverse demographic responses to habitat alterations because of differences in behavior, vulnerability to small scale environmental change and habitat specialization (reviewed by Silva 2001). Rosenblatt et al. (1999) assessed the impact of forest fragmentation on mammalian diversity and distribution in row crop agriculture in east-central Illinois. Their study suggests that species respond differently to the fragmented landscape based on a combination of habitat preference and dispersal ability. In general, although the existence of edge effects is widely accepted, the ecological response to edge often varies with definition of what an edge is, how edge effects are measured, and which species are studied (Murcia 1995).

Reducing the total area of remaining habitat can directly affect the population size of native species and increase local extinction rates (Krebs 1994). Top predators are particularly sensitive to this alteration because of their large ranges, low numbers and persecution by humans (Woodroffe & Ginsberg 2000). The loss of top carnivores from communities can disrupt food webs through trophic cascades or 'mesopredator release' that alter predator-prey interactions (McLaren & Peterson 1994; Crooks & Soulé 1999).

The degree of fragmentation and isolation of remaining habitat determine the magnitude of their effects on surviving natural communities. Habitat fragmentation is often modeled on concepts from the equilibrium theory of island biogeography which

suggests that populations on islands are characterized by reduced immigration and emigration due to their inherent isolation (MacArthur & Wilson 1967). These models are based on the assumption that forest fragments are habitat islands and they will experience processes similar to oceanic islands. A direct comparison of habitat fragments to islands rests on the assumption that suitable habitat patches are completely isolated from one another by hostile habitat (reviewed by Andren 1994). However, depending on the species in question, habitat fragments typically exist in a matrix of hostile, marginal and satisfactory patches. Habitat patches are therefore part of a larger landscape mosaic, and the ecological response to fragmentation will not only be a function of patch size and isolation but also the type of adjacent matrix (Andren 1994). Understanding how ecological communities respond to fragmentation attributes such as increased edge effects, reduction of patch area, and altered food webs is critical to our understanding of how human activities affect natural systems.

1.2 Trophic Cascades and Habitat Alteration

Trophic cascades are defined as reciprocal predator-prey effects that alter the abundance, biomass or productivity of a population, community, or trophic level across more than one link in a food web (Pace et al. 1999). Top-down trophic cascades in terrestrial systems are usually described as the indirect impacts of carnivores on plants through a shift in herbivore abundance or activity (Holt 2000). Carnivores can affect the impact that herbivores have on plants in two ways (Abrams 1996). They can cause changes in herbivore density by predation which may result in the reduction in the number of herbivores feeding on plants (Beckerman et al. 1997). Or, the presence of predators in itself could represent a risk of predation that would limit herbivore prey foraging behavior and thus reduce the impact on the plant community (reviewed by Beckerman et al. 1997). Although a large body of ecological research has shown that carnivores can have strong direct effects on the structure and dynamics of herbivore prey communities via predator-prey interactions (Sih et al. 1985; Schoener 1993; Schmitz et al. 2000), the strength of the indirect impact of carnivores on plant communities remains controversial. Schmitz et al. (2000) investigated the occurrence of trophic cascades in terrestrial systems by conducting a comprehensive review of studies that detected trophic cascades under natural field conditions. They found that although vertebrate carnivore-herbivore relationships can have important effects on plant biomass, experimental evaluations of these effects are still lacking (Schmitz et al. 2000).

Although the existence of terrestrial trophic cascades is still highly debated, a few studies of top down trophic cascades suggest a strong relationship between vertebrate predators and the plant community. McLaren & Peterson (1994) examined food chain control by wolves in Isle Royale National Park in Michigan, and established that moose density was largely determined by wolf population and predation. Additionally, the authors inferred that reduction of this herbivore population by wolves has led to a dramatic decrease in balsam fir herbivory by moose, with corresponding changes in plant communities across the landscape. Terborgh & Wright (1994) observed that the removal of top predators from reservoir islands in Venezuela dramatically increased the population of mammalian herbivores. They suggest that with the absence of top predators, recruitment via seedlings and saplings of canopy tree species decreases due to increased herbivore abundance. Thus, there is an indication that the removal of top

predators may lead to an increase in the abundance of mammalian herbivores and that this may have a long term affect on forest dynamics.

In fragmented landscapes, carnivores are particularly vulnerable to local extinction because of their natural rarity, large home ranges and potential for direct conflict with humans (Woodroffe & Ginsberg 1998). Despite the potential importance of top predators in the structure and function of ecological communities, few studies have documented their effects at multiple-trophic levels. This is particularly true in fragmented landscapes where top predators are most susceptible to extinction.

Interest has risen in a version of trophic cascade theory applied to fragmented habitats. The 'mesopredator release hypothesis' (Soulé 1988) was tested by Crooks & Soulé (1999) in a highly fragmented southern California scrub habitat. They predicted that the absence of top predators (coyotes) would lead to increased numbers of smaller-bodied carnivores (cats, raccoons, striped skunk, gray fox, opossum), termed 'mesopredators', that are principle predators of birds and other small vertebrates. They found direct evidence of both coyote predation on mesopredators and mesopredator predation on native birds (Crooks & Soulé 1999). Additionally, they found that mesopredators not only avoided coyotes within fragments, but also avoided sites in fragments where coyotes were most active (Crooks & Soulé 1999). These results thus indicated that the absence of coyotes resulted in elevated numbers of smaller carnivores and increased predation on native birds.

This hypothesis has not been extensively tested and the results of the few available studies are controversial (Crooks & Soulé 1999). However, it is logical that top predators could have an effect on lower trophic levels in fragmented landscapes through mesopredator release. This hypothesis could also be extended to include other trophic responses such as small mammal abundance and seed predation. Integrating these other potential ecosystem effects would strengthen our understanding of how top predators affect ecological communities in fragmented landscapes.

1.3 Influence of Seed predation on Plant Communities

Many plants suffer loss of seeds to predation by a wide range of animals (Janzen 1971, Harper 1977). Animals that feed on seeds or other reproductive parts directly reduce the plant's reproduction and may kill the plant (Fletcher et al. 2001). Small granivorous mammals are capable of strongly inhibiting seed survival and tree recruitment in both temperate and tropical forests (in Logiudice & Ostfeld 2002; Ostfeld et al. 1997; Hulme & Borelli 1999). Gutierrez et al. (1997) found that exclusion of the principal rodent herbivore and its vertebrate predators had significant effects on the relative abundance of several plant species in a semiarid Chilean Mediterranean site. Experimental exclusion of herbivores was associated with increased cover of some shrubs and a perennial grass and decreased cover and seed densities of several exotics and ephemerals (Gutierrez et al. 1997).

In the northeastern United States, depredation on seeds and seedlings by white-footed mice (*Peromyscus leucopus*) and meadow vole (*Microtus pennsylvanicus*) plays an important role in regulating the colonization of old fields by trees (Manson 1999; Mittelbach & Gross 1984; Gill & Marks 1991; Ostfeld et al. 1997). In a study of tree and shrub colonization of old fields in central New York, Gill and Marks (1991) found that seed predation by mice under the cover of herbs was an important process regulating the

relative abundance and spatial distribution of seeds after dispersal. Additionally, they found that seed predation reduced the probability of survival from dispersal through successful emergence to almost zero percent.

The results of these and other studies suggest that granivores have a substantial influence on tree seed survival. Understanding the interactions between small mammal herbivores and the vegetative communities they inhabit may be essential for predicting future community and landscape changes (Manson & Stiles 1998; Holt 2000; Manson 1999).

1.4 Habitat Fragmentation and Trophic Responses in the Albany Pine Bush

1.4.1 Fragmented State of the Albany Pine Bush

The Albany Pine Bush is a globally rare, pitch-pine scrub oak community in east-central New York. Historically, the Albany Pine Bush extended over 40 square miles between Albany and Schenectady and north to Glens Falls, New York (Albany Pine Bush Preserve Commission 1995). Presently, the Albany Pine Bush (APB) encompasses approximately 19 square miles in Albany County. Although highways, shopping centers and suburban developments have fragmented most of the original community, a few remnants still exist from Albany to Glens Falls (Figure 1). For a summary of the history and protection of the Albany Pine Bush see Zantopp (2000).

Within the APB, the Albany Pine Bush Preserve (APBP) is a small protected area of about 2,400 ha of undeveloped land (APBPC 1995). This remaining area is highly fragmented and situated in a matrix of suburban and urban development (Figure 1). Isolation of these fragments is amplified by railroad tracks, power line rights-of way and major highways and are being encroached upon by suburban housing, commercial development and a landfill (Gill 1997). Initial acquisition of land for the APBP from 1970-1994 increased the perimeter-area ratio of the whole preserve (Figure 2). It is only recently, 1995-1999, that this ratio has begun to decline. This level of fragmentation has modified many of the natural processes that have shaped this ecological community (Gill 1997). Edge effects are reducing the effective interior preserve area by altering the environment and ecological processes. For example, Gill (1997) observed higher temperatures, lower relative humidity and higher species diversity at preserve edges, consistent with studies of closed canopy forests. However, he also found that these edge effects varied in response to the diversity of vegetation types and land uses around the preserve.

In addition to the larger protected areas, smaller, privately owned patches of APB remain (Figure 1). These remaining patches have little to no interior forest and are generally surrounded by suburban development. The fragmentation of the Albany Pine Bush into both large and small fragments, surrounded by suburban development, creates a natural experiment in which to test the influence of human activity on ecological interactions.

1.4.2 Putative Food Webs in the Albany Pine Bush

The dominant ecological community within the boundaries of the APBP is fire-adapted pitch pine-scrub oak barrens (Reschke 1990). However, the landscape is extremely heterogeneous and is interspersed with other types of communities such as pine barrens, vernal ponds, pitch pine-oak forests, pine northern hardwood forests, successional northern and southern hardwoods, ravine forests and red maple-hardwood (Reschke 1990). This rare inland pitch pine/scrub oak barrens community is host to a number of unique and threatened species. In particular, the federally endangered Karner blue butterfly (*Lycaeides melissa samueli*) is closely associated with the Pine Bush (Zaremba et al. 1991). The butterfly depends on the open, sandy areas that are vital for its obligate larval host plant, blue lupine (*Lupinus perennis*). The APBP also harbors two rare natural communities and fourteen other rare insects (The Nature Conservancy 2002). Additionally, the eastern coyote (*Canis latrans*) has moved into the area and established populations in the APBP within the last ten to fifteen years. While initial established populations were low, preliminary results from the New York State Museum indicate that they now exist in relatively high numbers in this suburban-forest preserve (D. Bogan, unpublished data).

The arrival of coyotes in this area may have significant implications for the structure and function of food webs in the Albany Pine Bush. The presence of coyotes in this system would position them atop the food chain and could influence the trophic response of both smaller carnivores and their prey (Figure 3). If the increase in coyotes influences population dynamics of other carnivores, a cascade of ecosystem effects may occur (Gomper 2002). However, studies of the impact of coyotes on trophic interactions are currently unavailable in the Northeast (Gomper 2002). Although coyotes may play an important role in the Albany Pine Bush and in other suburban areas across the Northeast, no studies have examined their influence on trophic interactions.

In addition to affecting local ecosystem ecology, the increase of coyotes in a suburban landscape will increase human-coyote interactions. Coyotes are known to prey on domestic animals (Crooks & Soulé 1999) and as coyote populations increase so will pressure from the public to control them (Gomper 2002). With suburban development completely surrounding the APBP, the increase of coyotes in the area will not go unnoticed.

The isolated habitat patches and the recent arrival of coyotes in the Albany Pine Bush offer a unique landscape in which to study how and whether habitat fragmentation influences terrestrial trophic cascades. Little research has been published on the ecology of urban/suburban coyotes and, until now, there have been no studies conducted on the APB coyotes and their possible influences upon smaller carnivores and their prey. In addition, the influence of seed predation on plant regeneration may be of particular importance to the conservation of plant communities in the Albany Pine Bush. Pitch pine (*Pinus rigida*) regeneration is a major concern for managers and seedling densities are low in the preserve. Blue-lupine and New Jersey tea (*Ceanothus americanus*), important species for the Karner blue butterfly, have very low regeneration. Although the importance of seed predation on plant communities is well documented, no studies have examined the role of seed predators on these and other plant species in the APB.

1.5 Objectives

The purpose of this study was to experimentally evaluate small mammal abundance and seed predation rates in relation to edge effects and carnivore-mediated trophic cascades in the Albany Pine Bush Preserve by focusing on the following objectives:

1. Characterize the small mammal community of the APB in order to:
 - A. Record species composition and relative abundance of small mammals with respect to habitat fragmentation.
 - B. Experimentally determine seed predation pressure on native seeds.
 - C. Indicate which species are eating native seed species and determine seed preferences.
2. Draw from separate ongoing studies (R. Kays & D. Bogan, unpublished data) of carnivores that:
 - A. Document the carnivore species present.
 - B. Quantify activity in each area by coyotes and smaller carnivores.
3. Test whether habitat fragmentation influences the small mammal community through:
 - A. Area effects mediated through coyotes.
 - B. Edge effects independent of area.
4. Examine relationships among carnivore activity, small mammal abundance and seed predation rates.

I predicted that:

1. Large fragments will have higher coyote activity, which will limit mesopredators, and increase small mammal abundance and seed predation.

2. Small fragments with high mesopredator populations will have low abundances of small mammals and corresponding low levels of seed predation.
3. Small mammals will exhibit detectable differences in seed preference and predation rates.
4. Small mammal abundance and related seed predation rates will exhibit detectable differences at the interior and edge of large fragments.

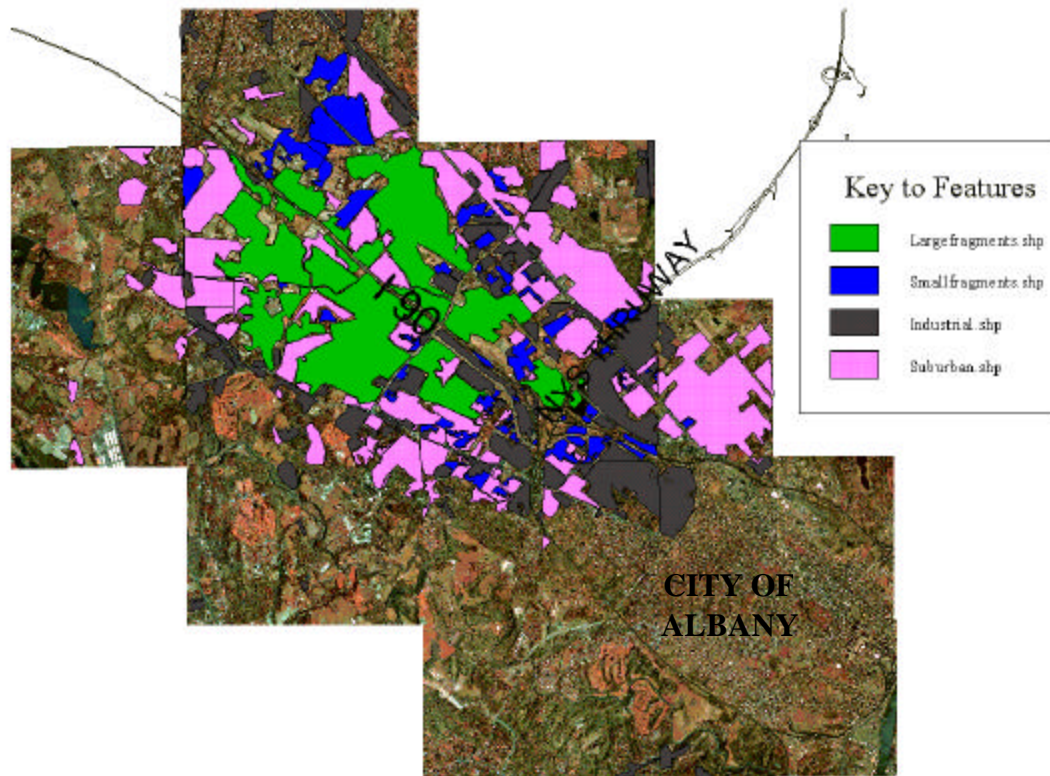


Figure 1. Digitized view of the Albany Pine Bush showing surrounding development. Digital Orthoquad images from 1990. Large Fragments are mostly protected preserve, small fragments are mostly privately owned pine bush fragments.

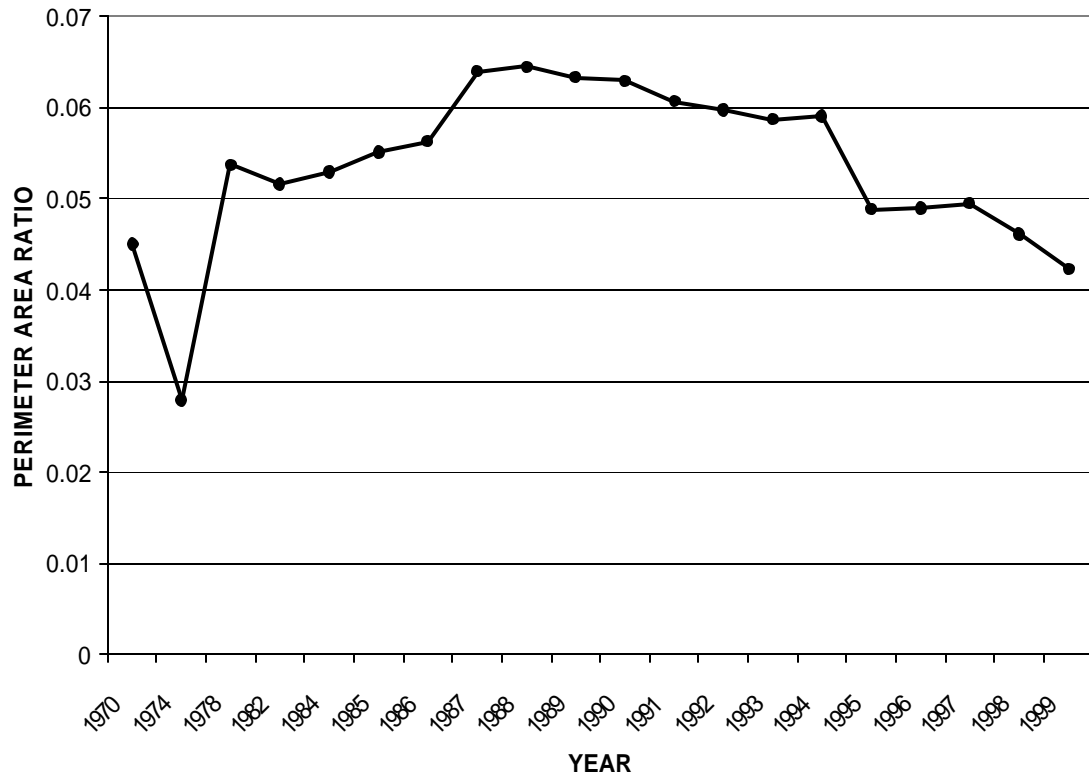


Figure 2. Cumulative perimeter/area ratio of land acquired for the Albany Pine Bush preserve from 1970-1999. From Zantopp (2000)

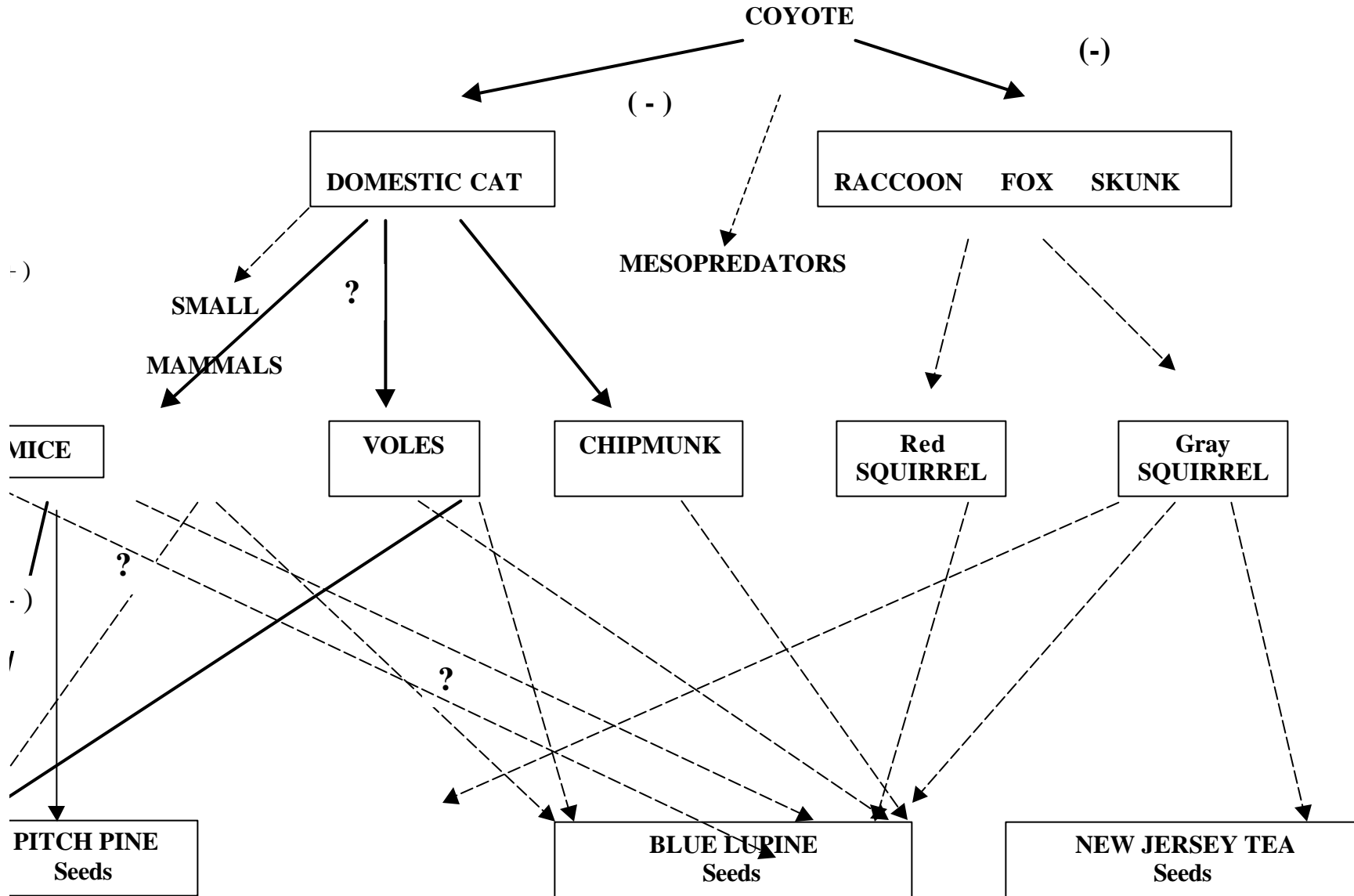


Figure 3. Diagram of possible trophic interactions in the Albany Pine Bush. Dotted arrows = unknown relationship

2 Methods

2.1 Study Sites

This study was conducted in both publicly and privately owned forest fragments of the Albany Pine Bush, Albany, New York (Figure 1). Sites were chosen to match the following criteria: (1) Even distribution of both large and small fragments (2) similar vegetation type (3) surrounded and bisected by suburban development. Fragments were classified as either 'large' (area > 40 ha, perimeter/area < .007) or 'small' (area < 12 ha, perimeter/area > .025) (Table I). Because there may be different ecological responses at the center and edge of large fragments, sampling in most of the large fragments occurred at both the center (center of grid >100 m to edge) and edge (center of grid <100 m to edge) of each site. Although imbedded in a heterogeneous vegetative landscape, all study sites were dominated by mixed woods habitat. There were therefore three site treatment types: Large Center (LC), Large Edge (LE) and Small (S).

Table I. Characteristics of fragments and study sites (LC = Large Center, LE = Large Edge, S = Small fragments)

Fragment	Area (ha)	Number of traps	P/A ratio	Size Class	Site Type
1	397.7	49	0.003	Large	LC
2	397.7	49	0.003	Large	LE
3	381.8	49	0.004	Large	LC
4	381.8	49	0.004	Large	LE
5	134.6	49	0.005	Large	LC
6	134.6	49	0.005	Large	LE
7	119.6	49	0.006	Large	LE
8	61.6	49	0.006	Large	LC
9	61.6	49	0.006	Large	LE
10	58.4	49	0.006	Large	LC
11	58.4	49	0.006	Large	LE
12	43.8	49	0.007	Large	LE
13	10.9	49	0.029	Small	S
14	9.8	47	0.026	Small	S
15	8.5	38	0.019	Small	S
16	5.8	49	0.03	Small	S
17	5.0	35	0.02	Small	S
18	4.3	26	0.034	Small	S
19	3.8	19	0.029	Small	S
20	2.6	30	0.041	Small	S
21	1.4	14	0.045	Small	S

2.2 Characterization of the Small Mammal Community

Track tube surveys (Glennon et al. 2002) were conducted from June-August 2001. Tracking tubes were constructed of metal rain gutter with removable aluminum plates. Ink-pads were fixed to both ends of the plate and clear contact paper between the ink pads to record small mammal prints in the tube (Figure 4). Track tube surveys are an alternative technique to live-trapping to assess the composition and relative abundance of small mammals (Appendix A). Tubes are baited and set out in uniform trapping grids and the presence of tracks in each tube is an indicator of relative abundance of the identified

species. I also conducted live trapping in each of the large fragments from June-October 2001 to develop a reference collection of footprints of local species. After an animal was trapped, it was run down an elongated track tube and then released. This created a permanent record of known species tracks. Additionally, print guides created by M. Glennon (2002) were used (Appendix B).

Most prints could be determined to the species level. Although I was not able to distinguish *Peromyscus* spp. (Deer/White-footed mouse) from *Clethrionomys gapperi* (Red backed vole), *Clethrionomys* was never caught during live-trapping in large fragments and it was thus considered not present or extremely rare. Prints of *Sciurus carolinensis* (Gray squirrel), *Tamiasciurus hudsonicus* (Red squirrel), *Tamias striatus* (Chipmunk), *Microtus pennsylvanicus* (Meadow vole), *Napeozapus insignis* (Woodland jumping mouse), *Blarina brevicauda* (Short tailed shrew), and *Glaucomys sabrinus* (Flying squirrel) could all be distinguished (Appendix B). A list of the mammal species I detected and their common and referenced names are given in Appendix C.

A grid design of 7 x 7 tubes with 20 m spacing between each track tube (total grid area = 1.96 ha) was used at LC and LE sites. Spacing the track tubes at 20 m distances is a standard estimate of home range size in *Peromyscus* spp. and thus gives independence. Small sites were sampled using track tubes in smaller, irregular grids with tubes placed at 20 m intervals, arrayed to sample as much of the site as possible. The large grids all contained 49 tubes, while the smallest grids could hold only 14 (Table I). Once in place, tubes were baited with peanuts, examined and rebaited after 2 days, and examined a second time and removed after 4 days. Contact paper strips with white paper served as the permanent record of tracks from each tube.

Small mammal density was inferred from the relative frequency of track tube use (occupancy rates). Occupancy is not an exact description of density because it is impossible to determine if we recorded multiple individuals of a species per tube, or whether the same individual of one species is visiting the tubes on multiple days. Prints of a single species in a tube are therefore counted as one individual and relative frequency was calculated by the number of prints per species per tube/number of possible tubes.

Fig 4. View of track tubes and plate. Photos courtesy of Glennon (2202)



2.3 Seed Predation Experiments

Seeds of native plants were chosen on the basis of their importance to APBP managers and on the suspicion that regeneration of these plants is impeded at the seed or seedling stages. Pitch pine was chosen because it is the dominant native tree species within the preserve and because it may not be regenerating sufficiently to maintain its population (Gill 1997). Blue lupine and New Jersey tea were chosen because they are food plants for the federally endangered Karner blue butterfly and because seedling regeneration is low throughout the preserve. Seed predation experiments were conducted between September and October 2001, using the same grid design and locations outlined above but using native plant seeds as bait. The Albany Pine Bush Commission collected New Jersey Tea and blue lupine seeds in the Albany Pine Bush Preserve in 2001. Pitch Pine seeds were collected by Dr. George Robinson from 1995-1997 and stored under refrigeration; they were recently tested and exhibited an 80 percent germination rate. Ten pitch pine, blue lupine, and New Jersey tea seeds were alternately placed in tubes throughout the grid. Tubes were checked after 2 days and the number of seeds predated was recorded. Predation was indicated by either complete or partial consumption of the seed (with evidence of granivory in the tube) or if the seed was completely removed. Tubes were rebaited to hold a full 10 seeds as necessary, recorded and removed after 4 days. Again, contact paper strips served as the permanent record of tracks from each tube.

Individual species could be distinguished from tracks and most tubes visited had evidence of only one small mammal species. However, when multiple species visit a tube it is impossible to determine species-specific seed predation. Therefore, in my analyses, I distinguish between seed predation attributable to single or multiple species.

2.4 Carnivore Monitoring

All carnivore data were collected by scientists from the New York State Museum under the direction of Dr. Roland Kays. Nine coyotes were monitored using live-trapping and radio-telemetry. Triangulated radio telemetry locations were collected randomly from 9 April 9, 2001 – 9 April 2002 (D. Bogan, unpublished data). All locations were partitioned by edge (<100 m from edge) and interior (>100 m from edge) among large fragments studied (Figure 5). Smaller carnivores were surveyed with scent stations. Five motion sensitive cameras from Camtrakker® were placed at all study sites (LC, LE, S) for one night each. Each station was baited with a fatty acid scent tablet. Carnivore attendance was recorded by tracks in a 1 m diameter patch and/or a photograph taken.

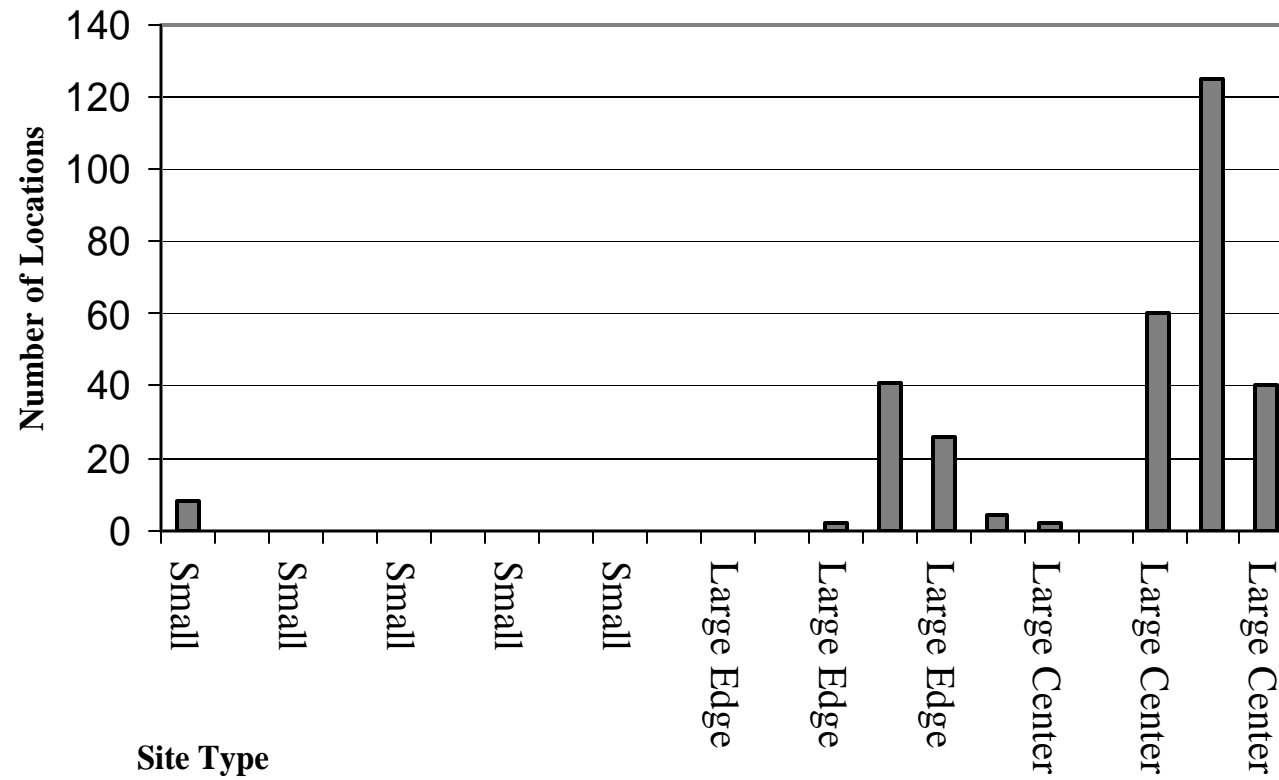


Figure 5. Number of coyote telemetry locations from 2001-2002 partitioned by edge (<100 m from edge) and interior (>100 m from edge) among large fragments studied (D. Bogan and R. Kays unpublished) (See Table I).

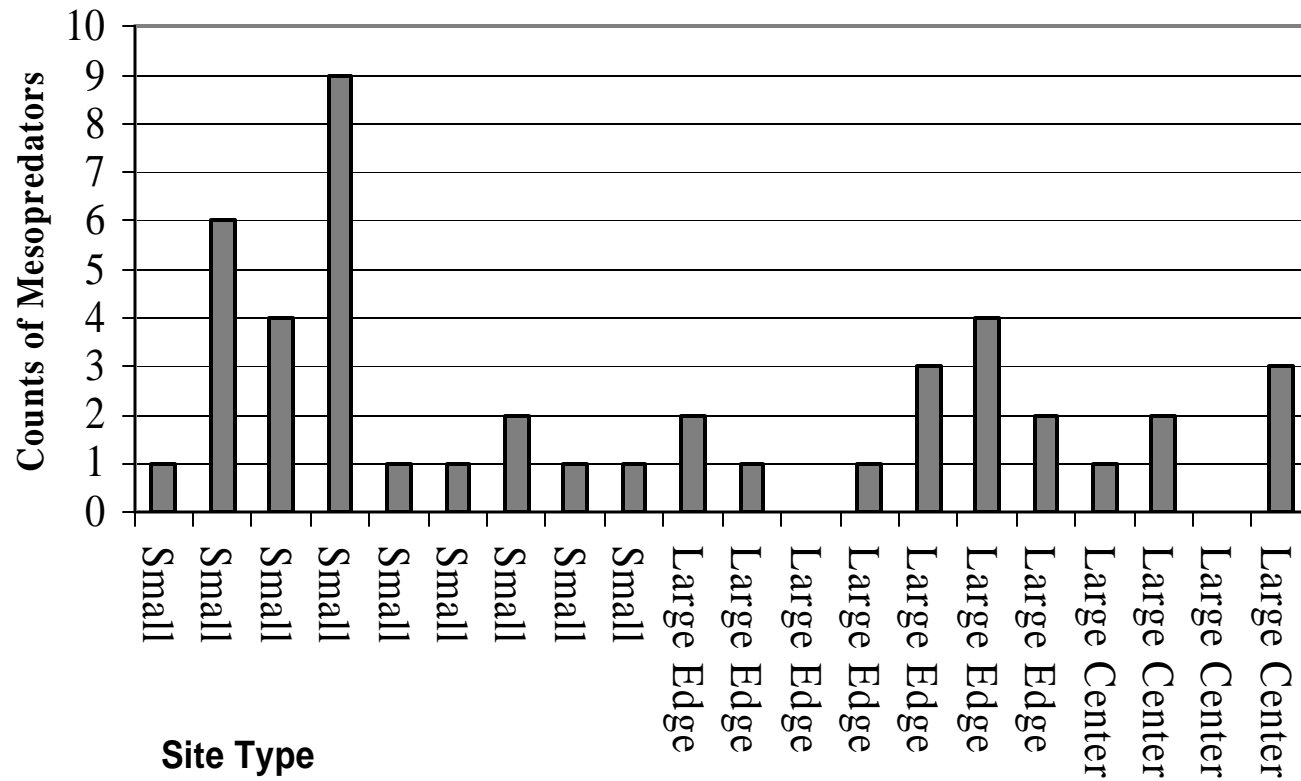


Figure 6. Number of mesopredators (Fox, raccoon, cats) detected by motion sensor cameras for each site type. Data courtesy of the New York State Museum

2.5 Analytical Methods

To test for an association between species richness and fragment area, I used linear regressions on $\ln(\text{area})$ and the number of mammal species recorded, for both summer and fall sampling, in all habitat fragments. For each Large Edge and Large Center site a cumulative number of mammal species were used ($N = 13$). Slopes of the regressions were evaluated for comparison with other species/area studies. All statistical tests were performed using SYSTAT 9.0 unless otherwise indicated.

To test my first and second hypotheses, I used 'occupancy rate' of track tubes baited with peanuts (summer) as an indicator of relative density for each species. Occupancy was calculated for each site as the number of species per tube/number of tubes per grid. This formula therefore yielded numbers greater than one when multiple species visited one track tube in locations where most tubes were visited. To determine if summer occupancy was significantly different among the three site types, a Kruskal-Wallis one-way was performed with total occupancy grouped by site type (Large Center, Large Edge, Small). Occupancy rates of the most abundant species were also analyzed in relation to site type.

Because occupancy rates in the summer may be different than 'occupancy rates' in the fall (differences in bait, seasonal and population fluctuations), occupancy rates were also calculated for grids using native seeds (fall). To determine if fall 'occupancy rates' were significantly different among the three site types, a Kruskal-Wallis test was performed with fall total rates grouped by site type (Large Center, Large Edge, Small). Again, data for the most abundant species were analyzed in relation to site type. As a general test for site similarity in abundance among species and between seasons, I used a Pearson correlation matrix using pairings of the most abundant species.

Carnivore activity was determined for coyotes as their number of occurrences from telemetry locations, and activity of smaller (meso) predators (cats, raccoons, foxes) was determined from counts of occurrences at camera traps. This work was conducted by other researchers, (R. Kays, unpublished, D. Bogan unpublished) and their summary data were used to characterize each site. Different levels of activity were determined according to relative differences in sampling abundance. For example, because the number of coyote locations were so variable, coyote activity was represented by the number of telemetry locations. On the other hand, cats were indicated as either high (>1 detected) or low (≤ 1 detected) and total mesopredators were indicated as high (≥ 2 detected) or low (< 2 detected) (Table II).

Table II: Triangulated radio telemetry locations for coyotes and number of camera trap detections per site for smaller carnivores. Mesos = (fox, raccoon, cat, skunk)

Site Type	# of Cats	# of Mesopredators	# of Coyote Locations
Large Center	0	3	40
Large Edge	1	2	4
Large Center	0	0	125
Large Edge	2	4	26
Large Center	0	0	60
Large Edge	2	3	41
Large Edge	0	1	2
Large Center	0	2	0
Large Edge	0	0	0
Large Center	0	1	2
Large Edge	0	1	8
Large Edge	1	2	0
Small	1	1	0
Small	0	1	0
Small	1	2	0
Small	1	1	0
Small	0	1	0
Small	5	9	0
Small	3	4	0
Small	5	6	0
Small	1	1	0

A principal components analysis (PCA) was performed to examine differences among treatments and is useful in describing environmental parameters. PCA uses correlations among multiple factors to arrange them in multivariate combinations to reflect their variance contributions reduced to fewer dimensions. This type of ordination allows comparison between variables that were not measured in the same units. I used the following variables from my sampling and carnivore data: (1) occupancy rates of the five most abundant small mammal species, (2) site type, (3) high/low activity of mesopredators, (4) high/low activity of cats, and (5) number of telemetry locations of coyotes all from Table II. I then used PCA to ordinate sites on the basis of treatment. In this analysis, eigenvalues indicate the variance explained by multivariate factors. The two most influential factors (2 highest eigenvalues) were used to ordinate each of the 21 sites according to treatment.

To test my third hypothesis, seed predation rates were calculated for each seed species for each site type as the proportion of total seeds taken. This proportion was calculated as seeds taken on day 1/10 + seeds taken on day 2/10 to yield a single predation rate for each seed species for each site type. To determine if seed predation rates differed significantly among the three site types, a Kruskal-Wallis test was run on the mean proportion of total seeds taken per site type (Large Center, Large Edge, Small). I then performed contingency tests (G-tests) with the overall number of seeds taken of each species to examine seed preferences and test whether the proportions of each type taken were the same. Contingency tests were also run for each native seed species across site type to test whether the proportions of seeds taken were the same at each site (Large Center, Large Edge, Small). Additionally, seed predation rates were calculated for each mammal species for each seed type. In these analyses, all tubes visited by more than one species were eliminated and seed predation rates were calculated for predation that could be attributed to only one mammal species.

I then compared summer total occupancy rates to related seed predation rates for each site type, treating summer rates as a measure of background densities independent of seed preference. A linear regression was used to test for a relationship between summer total occupancy and seed predation levels grouped by site type (Large Center, Large Edge, Small). Separate regressions were run for each major seed predator (determined by seed predation rates calculated for each mammal species) on background (summer) total occupancy rates and seed predation levels grouped by site type. This analysis aimed to detect whether the community of animals sampled using native seeds as bait differed from those sampled using standard bait.

Linear regression was used to examine the relationship between fall occupancy and seed predation rates grouped by site type (Large Center, Large Edge, Small). Regressions were used to test for a relationship between total estimated mammal density (pooled occupancy rates) and seed predation rates, according to site type.

To examine the relationship among small mammal occupancy, carnivore activity and seed predation, I used the significant environmental variables that emerged from the PCA to conduct a canonical correspondence analysis (CCA). This technique allows environmental variables and multiple species to be ordinated simultaneously (Ter Braak & Smilauer 1998). CCA chooses a combination of environmental data that maximizes the species–environment correlation by creating a linear combination of environmental variables. The output of the CCA can then aid in generating hypotheses to explain

evident patterns due to treatment differences. If these environmental variables are strongly related to seed predation, CCA will create an axis from these variables that makes response curves distinct (Palmer 2002).

3 Results

3.1 Species-Area Relationship

Among all study sites, I detected 8 mammal species. The linear regression of species on area was significant for summer track tube sampling (Fig. 7). The total number of species recorded ranges only from 2-7 and three species (*Napeozapus*, *Tamiasciurus* and *Glaucomys*) seemed to show a preference for the interior of large fragments but were rarely detected. The remaining mammal species are known habitat generalists and were found in almost all fragment sizes. The slope of the species/area relationship for fall sampling, when native seeds were the bait and fewer small mammal species were detected, was indistinguishable from zero (Fig. 8).

3.2 Small Mammal Abundance

Track tube use was very high for summer sampling with almost 90 percent of tubes in each grid visited. Although there seemed to be significant variability in total occupancy among site types, differences among treatments (Large Center, Large Edge and Small) were not significant (Fig. 9). *Sciurus* and *Peromyscus* were the most abundant species and their presence seemed to be site specific. For example, *Sciurus* appeared to prefer Center and Small sites while *Peromyscus* seemed much more abundant at the edge. However, differences in total occupancy for both *Sciurus* and *Peromyscus* across site types were not significant (Fig. 10a,10b) (*Sciurus*: $df = 2$ Chi-Sq = 3.051 $p = 0.217$ *Peromyscus*: $df = 2$ Chi-sq = 2.823 $p = 0.244$)

Track tube use in the fall was lower with only about 30 percent of tubes in each grid occupied. Although it appeared that total occupancy at LE sites were higher than at LC and S, differences among treatments were not significant (Fig. 11). However, a comparison of the abundances of the two most abundant species, *Peromyscus* and *Sciurus*, shows a contrasting pattern (Fig. 12a, 12b).

Significant correlations were evident in the comparisons of species abundance for fall and summer. *Sciurus* and *Peromyscus* exhibit a strong negative correlation for both sampling periods across all site types (Table III). Additionally, there was a strong positive relationship between *Peromyscus* and *Microtus*. I often found *Peromyscus* and *Microtus* tracks in the same tube for unknown reasons. Within each species, summer and fall abundance were negatively or weakly positively correlated, indicating that the overall estimates differed over the two sampling periods.

3.3 Species Ordinations and Treatments

The two first axes of the PCA explain 48 percent of the total variance (Fig. 13). Additional factors explained negligible variance and were not included. Factor 1 seems to be related to carnivore activity with both mesopredators and coyotes loading heavily on both the positive and negative axis. Additionally, site type and *Sciurus* load heavily on this factor however it is unclear how this is related. Factor 2 appears to be related to the relationship between *Peromyscus* and *Sciurus* which both load heavily on the positive and negative axis. This is consistent with the strong negative relationship exhibited by the correlation matrix described above. Both *Peromyscus* and total occupancy did not

respond to Factor 1. These environmental factors were then ordinated by site type (treatment variable removed) and arrayed on a biplot to validate experimental treatments (Fig. 14). Both factors contain little explanatory power with all site types evenly distributed across the axis for Factor 1 and 2 (Fig. 14). Plots of both types are well-spread over axis 1, whereas large and large edge cluster near zero on axis 2.

3.4 Seed Predation

3.4.1 Seed Preference

Seed predation rates were greater than 0 for all seed types among all sites, with the proportion of seeds taken greater than 0.20 for all seed species (Table IV). For tubes that were visited and had seeds removed, 40% had all seeds taken. The total number of seeds taken (3317) from visited tubes was 68% of the total possible seeds available (4820). The average number of seeds taken on day 2 (1.99) was only slightly higher than the average number of seeds taken on day 1 (1.76). As predicted, the proportion of pine seeds taken (0.38) was significantly higher than lupine and New Jersey tea (Table IV), a difference consistently observed at all study sites. When seed predation can be attributed to only one species (Table VI), *Peromyscus* accounts for the highest proportion of seeds taken (0.716).

3.4.2 Seed predation and edge effects

As I predicted, seed predation was highest for sites at the edge of large fragments ($df = 2$, Chi-sq = 7.268 $p = 0.026$). Overall seed predation of each seed species varied among site types. Seed predation rates were highest for each seed species at the Large Edge sites (Table V). This indicates that the edge effects observed for overall seed predation are independent of seed type.

3.4.3 Small Mammal Occupancy and Seed Predation

Estimates of background summer, small mammal densities were not related to seed predation rates, and in fact a negative trend was suggested (Fig 16). This does not support my first hypothesis that high small mammal abundance leads to higher rates of seed predation. However, a relationship between fall small mammal occupancy and seed predation was significant ($df_{1,19} F = 33.36 p = .0001$) (Fig 17), and consistently positive for each site type (Fig 18).

Species differences in fall occupancy rates were related to seed predation rates grouped by site type. *Peromyscus* showed a significant positive relationship between fall occupancy and seed predation for all site types (Fig 19). The relationship between *Sciurus* occupancy and seed predation was not significant and inconsistent among site types (Fig 20).

3.5 Canonical Correspondence Analysis

To examine the possible trophic interactions, a canonical correspondence analysis (CCA) was performed using the PCA structure that is related to environmental variables and treatment effects. Seed predation for each seed species was ordinated on this structure to graphically determine if patterns of seed predation can be linked to the

mammal community and carnivore presence. The relationship between seed predation and the environmental variables was weak for each seed type (Fig. 23a, 23b, 23c). Although the proportion of seeds taken by *Sciurus* responded slightly to factor 1, it is unclear whether this related to the presence of carnivores or is influenced by other landscape variables.

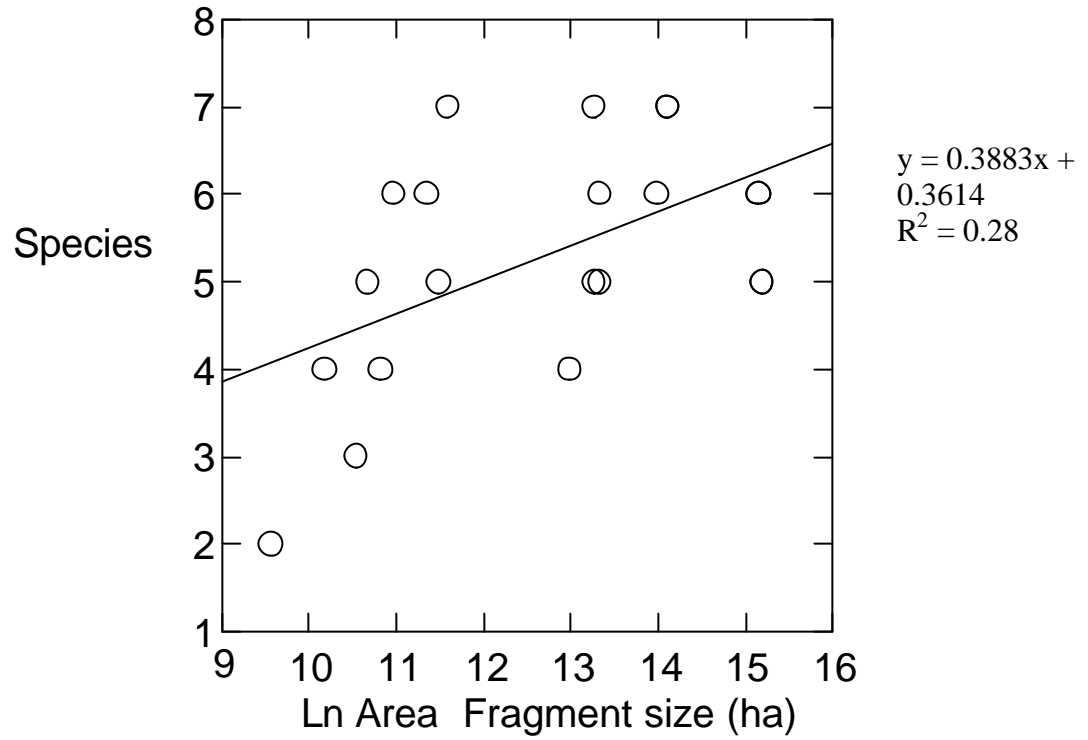


Figure 7. Species-area relationship for small mammal species detected during summer sampling using peanuts as bait in small and large fragments of the Albany Pine Bush (df_{1,13} F = 4.74 p = .048).

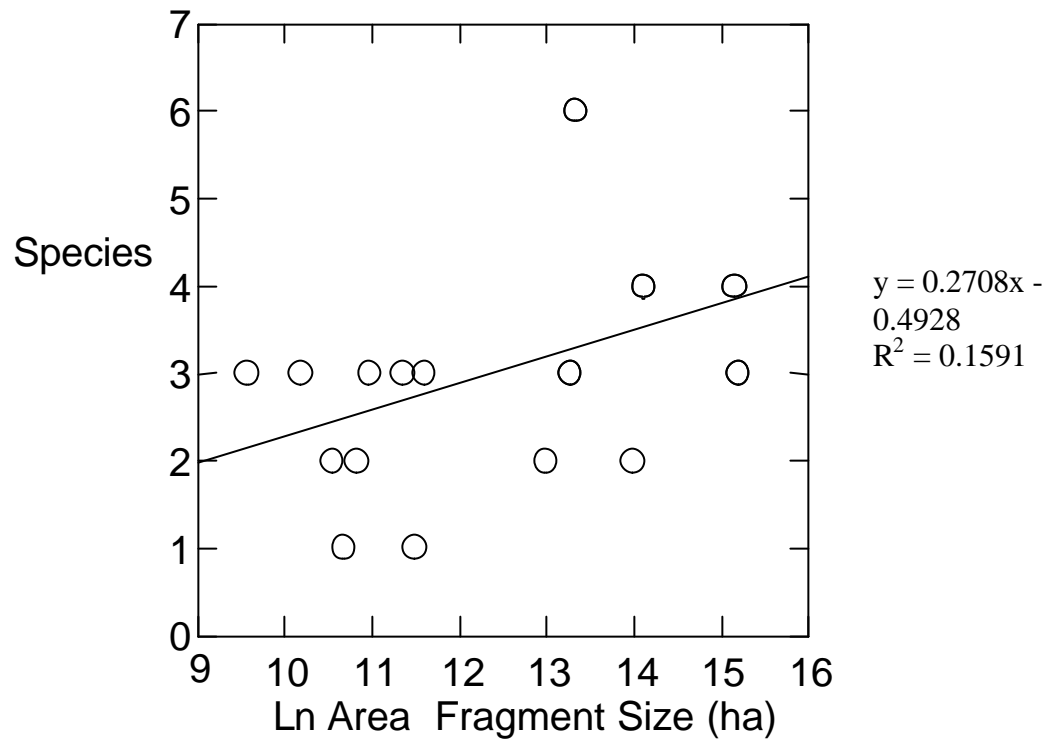


Fig 8. Species-area relationship for small mammal species detected during fall sampling, using native seeds as bait, in small and large fragments of the Albany Pine Bush (df_{1,13} F = 3.68 p = .07).

Table III. Pearson correlation matrix of species interactions for total occupancy of each species.

	<i>Sciurus</i> Summer	<i>Peromyscus</i> Summer	<i>Microtus</i> Summer	<i>Tamias</i> Summer	<i>Sciurus</i> Fall	<i>Peromyscus</i> Fall	<i>Microtus</i> Fall	<i>Tamias</i> Fall
<i>Sciurus</i> Summer	1.00							
<i>Peromyscus</i> Summer	-.208	1.00						
<i>Microtus</i> Summer	-0.014	0.452	1.00					
<i>Tamias</i> Summer	0.012	0.231	-0.329	1.00				
<i>Sciurus</i> Fall	-0.361	-0.183	0.035	0.187	1.00			
<i>Peromyscus</i> Fall	0.014	0.153	-0.210	-0.046	-0.640	1.00		
<i>Microtus</i> Fall	-0.046	-0.004	-0.153	0.077	-0.226	0.683	1.00	
<i>Tamias</i> Fall	0.055	0.034	-0.093	-0.291	-0.300	0.455	0.083	1.00

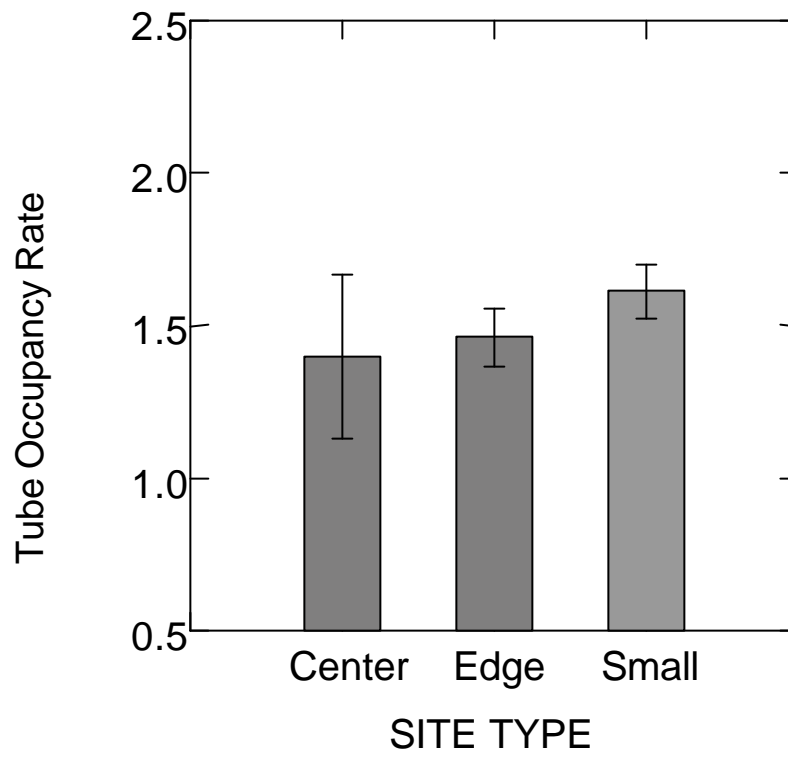


Figure 9. Mean small mammal occupancy rates for summer sampling of all species across site types (df = 2, Chi-Sq = 1.935, p = 0.38)

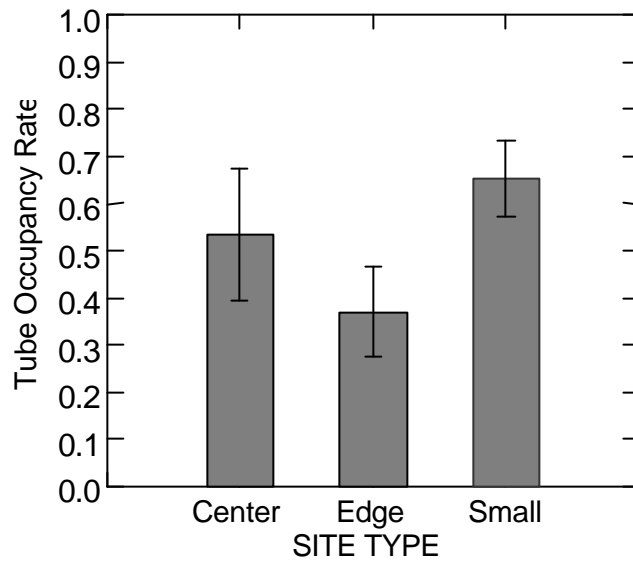


Figure 10a. Mean *Sciurus* occupancy rates for summer sampling across site types (df = 2, Chi-Sq = 3.051 p = 0.217)

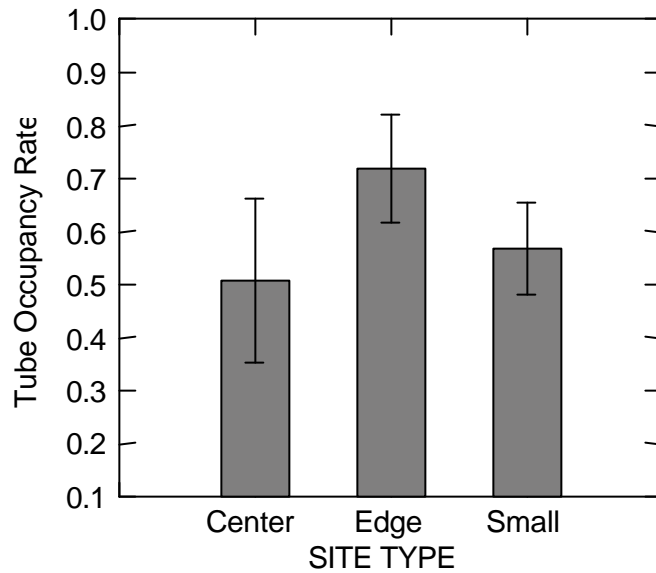


Figure 10b. Mean *Peromyscus* occupancy rates during summer sampling grouped by site type (df = 2 Chi-sq = 2.823 p = 0.244)

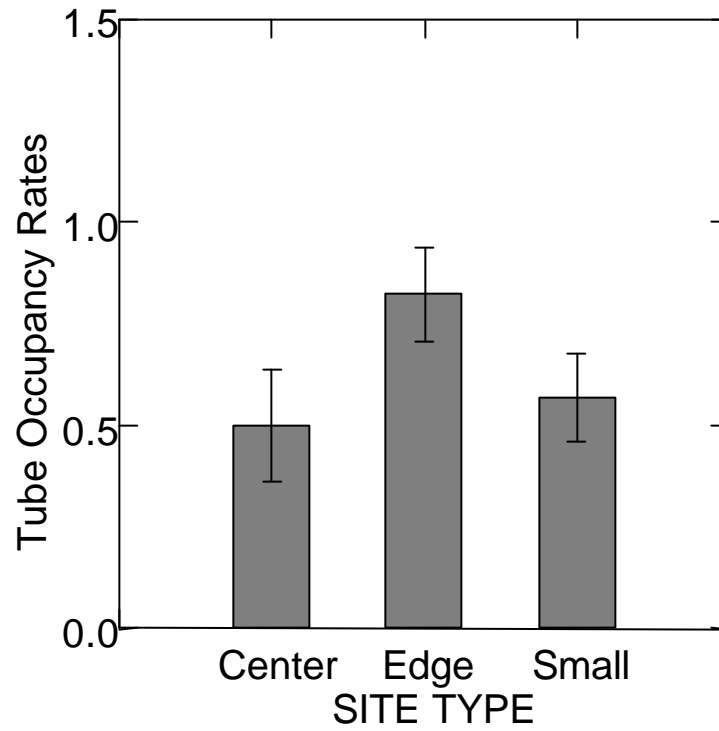


Figure 11. Mean small mammal occupancy rates (all species) for fall sampling (native seeds as bait) of all species across site types (df = 2, Chi-Sq = 4.88, p = 0.08)

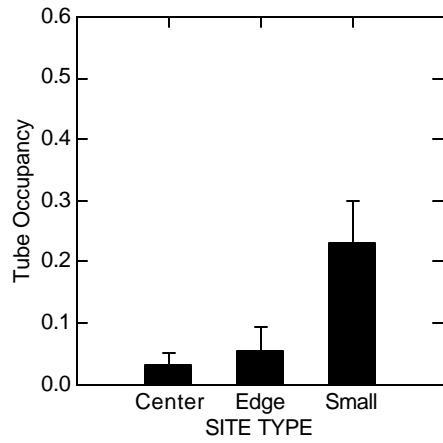


Figure 12a. Mean *Sciurus* occupancy rates for fall sampling (native seeds) grouped by site type (df = 2 Chi-Sq = 6.81 p = .033)

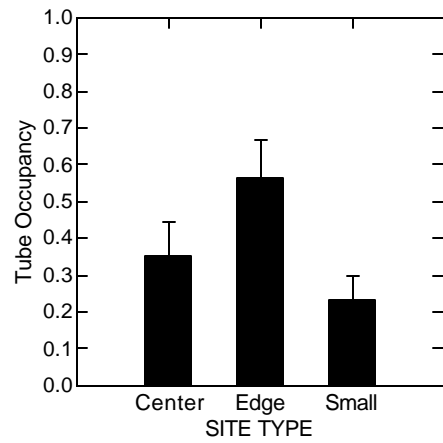
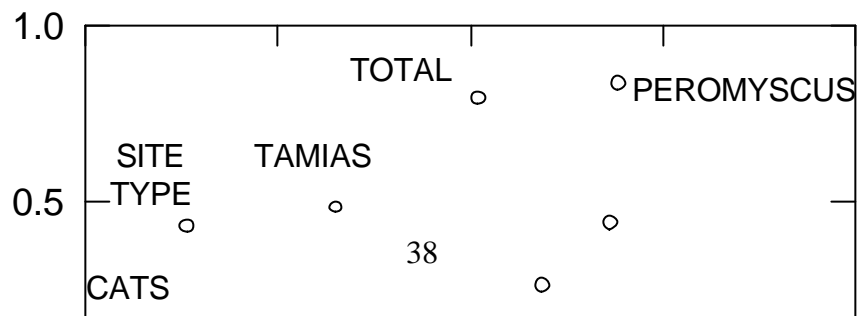


Figure 12b. Mean *Peromyscus* occupancy rates during fall sampling grouped by site type (df = 2 Chi-Sq = 7.059 p = .029)



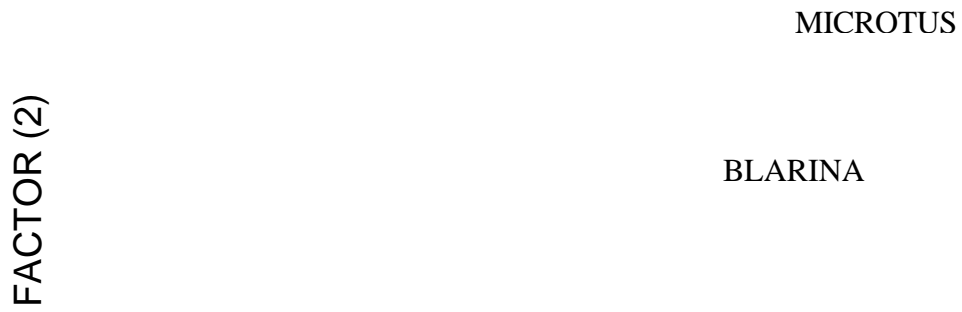


Figure 13. Factor loadings plot for PCA(Eigenvalues: Factor 1 = 2.525 Factor 2 = 2.233). Symbols refer to relative density of each indicated species based on track tube occupancy rates and carnivore activity. Additionally variables included were as follows: Total small mammal occupancy (TOTAL), Treatment type (SITE TYPE), Total counts of cats (CATS) and Total counts of mesopredators (MESOPREDATORS).

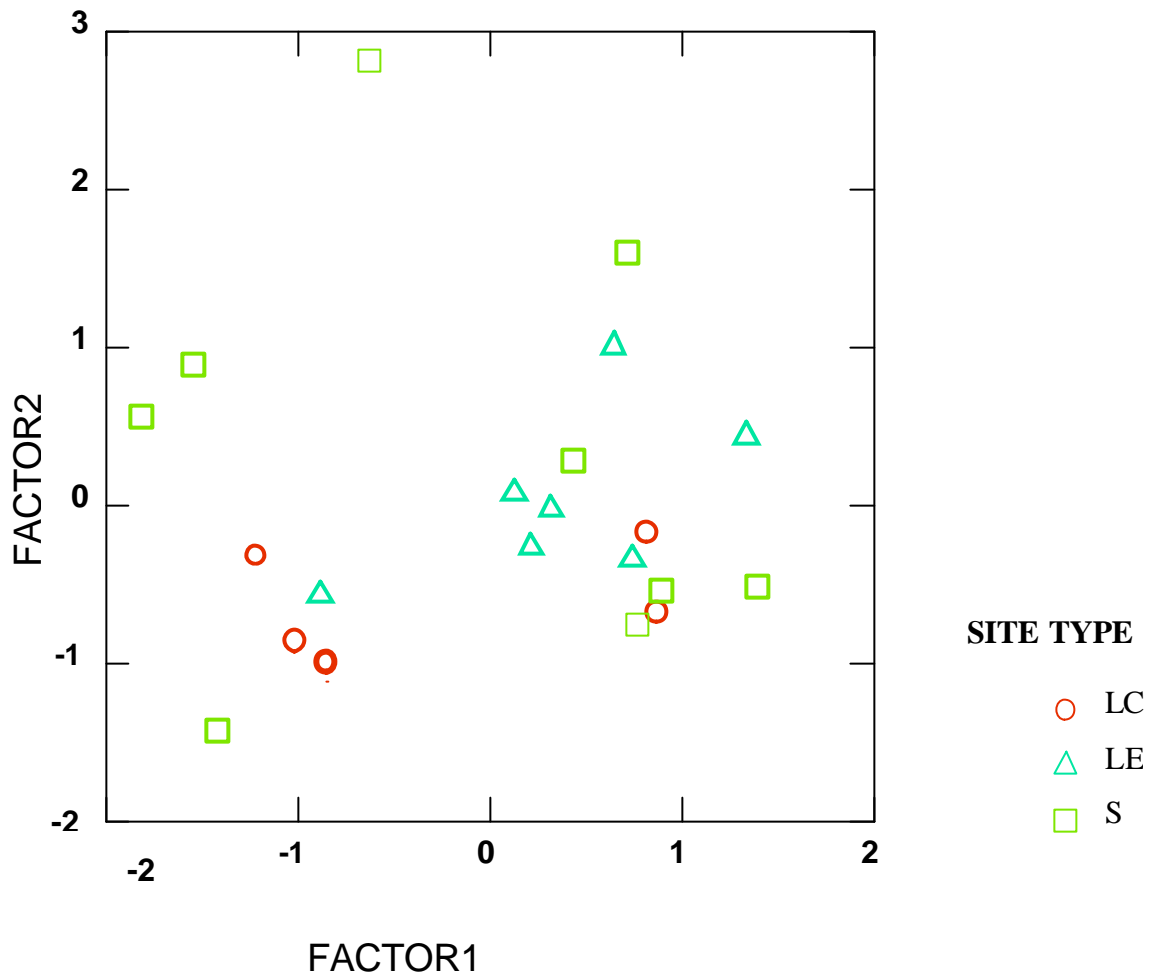


Figure 14. Ordination by treatment type, using PCA variables (Fig. 13), with treatment variable removed. Variables ordinated by site type: Large Center (LC), Large Edge (LE) and Small (S)

Table IV. Overall number of seeds taken for each seed species. Differences in proportion of seeds taken were significant ($df = 2$ $G=309.79$, $p=.0001$)

SEED TYPE	SEEDS OUT	PROPORTIO N TAKEN
PINE	3840	0.38
LUPINE	3840	0.20
NJ TEA	3840	0.26
TOTAL	11520	0.28

Table V. Proportion of pitch pine, blue lupine and New Jersey tea seeds taken at each site

SITE TYPE	PINE Seeds Out	PINE Proportion Taken	LUPINE Seeds Out	LUPINE Proportion Taken	NJ TEA Seeds Out
Large Edge	1640	0.53	1640	0.28	1590
Large Center	1040	0.26	980	0.14	505
Small	1160	0.29	1220	0.16	228
Total	3840	0.38	3840	0.20	270

Table VI. Proportion of all seeds taken by only one small mammal species.

SPECIES	PINE TAKEN	LUPINE TAKEN	NJ TAKEN	TOTAL TAKEN	PROPORTION OF TOTAL TAKEN
<i>Sciurus</i>	151	79	102	332	0.087
<i>Tamiasciurus</i>	21	5	4	30	0.008
<i>Peromyscus</i>	1233	658	848	2739	0.716
<i>Microtus</i>	212	97	96	405	0.106
<i>Tamias</i>	67	40	52	159	0.042
<i>Glaucomys</i>	1	11	9	20	0.005
<i>Napeozapus</i>	0	9	0	9	0.002
Unknown	19	2	31	52	0.014
TOTAL	1743	919	1166	3828	

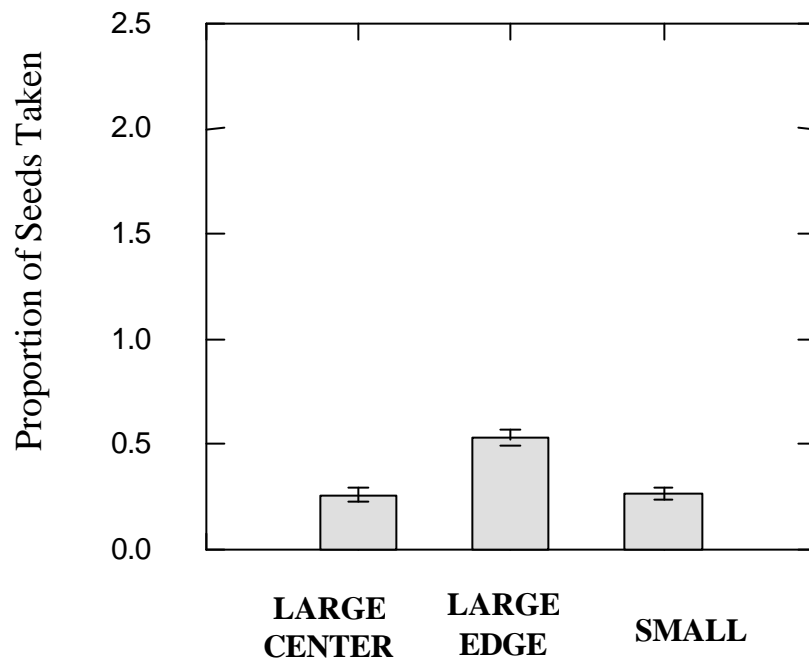


Figure 15. Mean proportion of seeds taken across site types (df = 2, Chi-Sq = 7.268 p = 0.026)

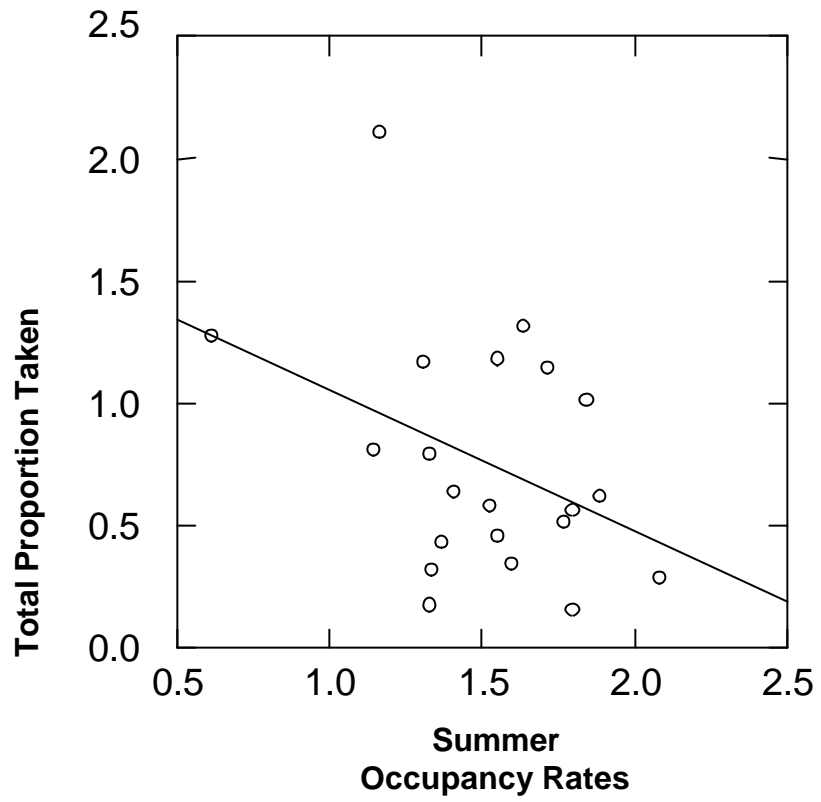


Figure 16. Scattergram of summer occupancy and total proportion of seeds taken. (Least squares linear regression: $df_{1,19}$ $F = 3.482$ $p = 0.078$ $R^2 = 0.152$)

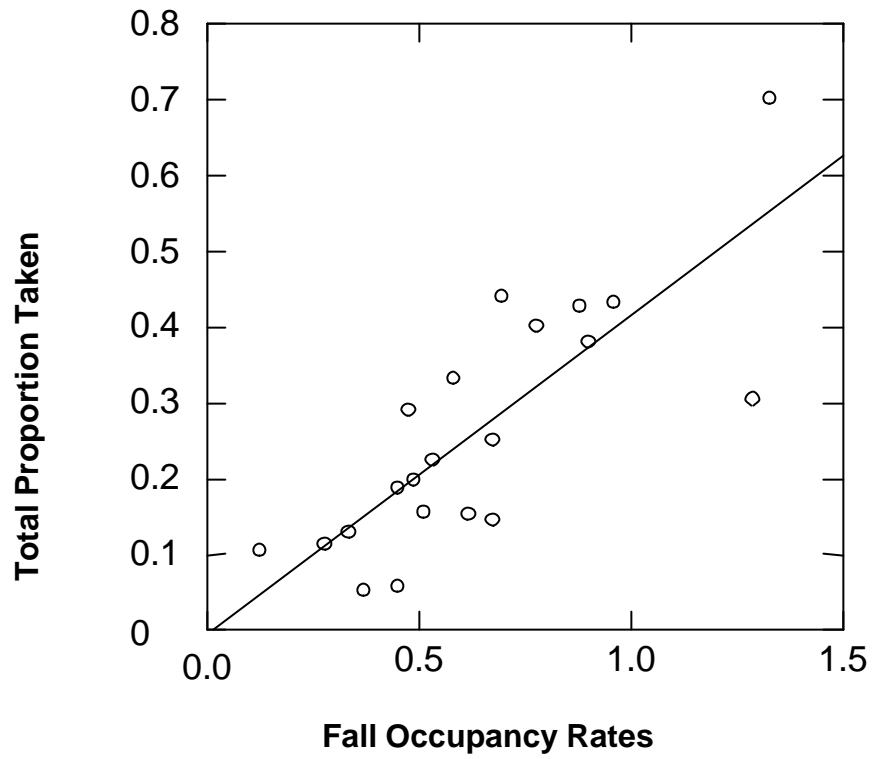


Figure 17. Scattergram of fall occupancy and total proportion of seeds taken (Least squares linear regression: $df_{1,19}$ $F= 33.36$ $p = .0001$ $R^2 = 0.637$).

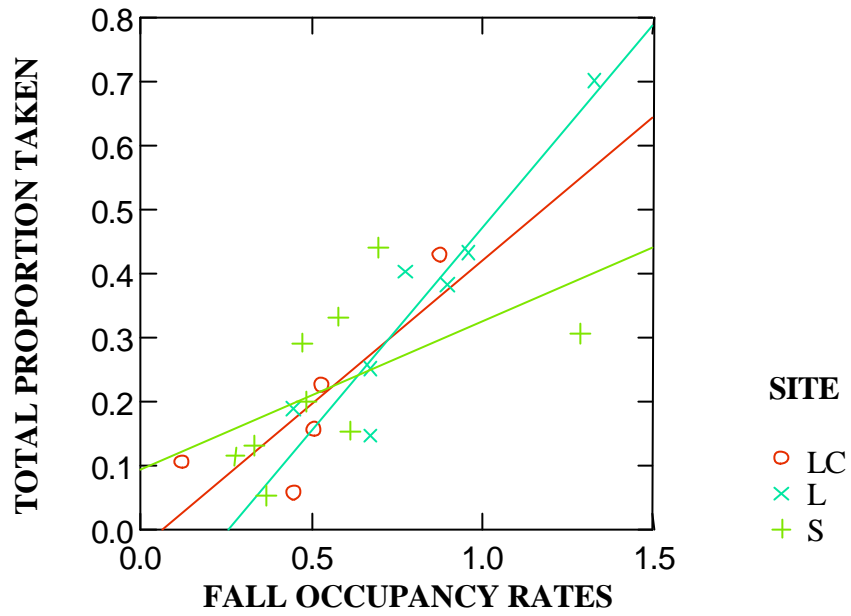


Figure 18. Scattergram of fall occupancy rates and total proportion seeds taken grouped by site type: Large Center (LC), Large Edge (LE) and Small (S).

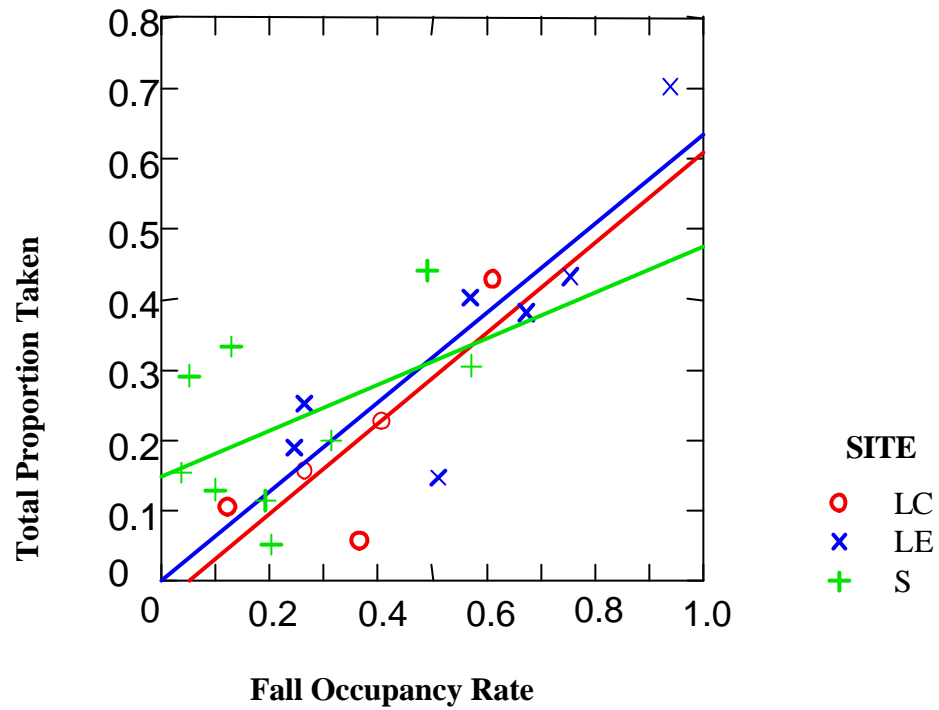


Figure 19. Scattergram of *Peromyscus* fall occupancy and total proportion of seeds taken site type: Large Center (LC), Large Edge (LE) and Small (S) (Overall pooled regression: $df_{1,19}$ $F = 24.64$ $p = .000$).

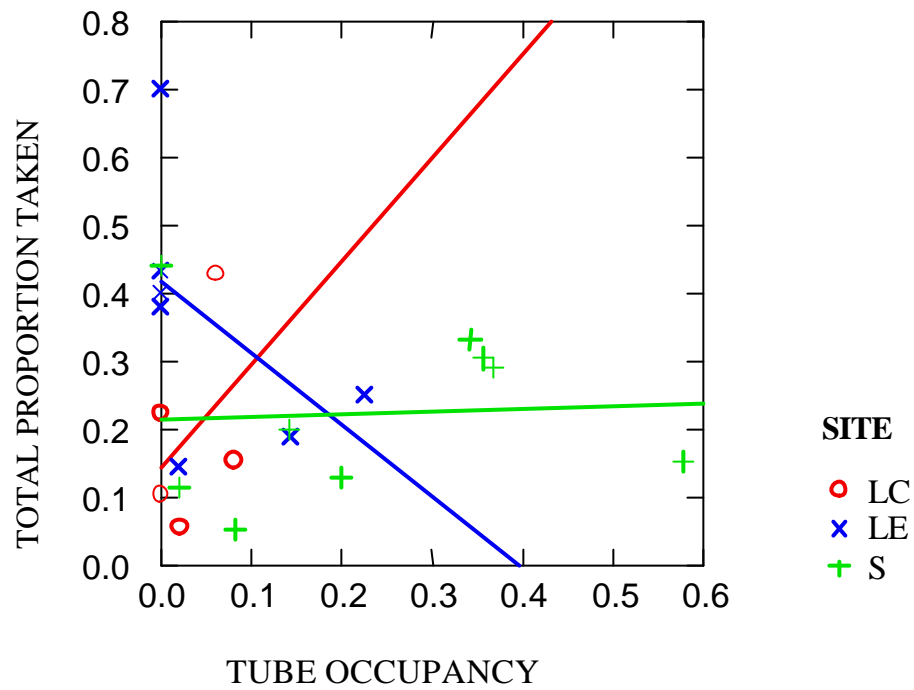


Figure 20. Scattergram of *Sciurus* fall occupancy and total proportion of seeds taken by site type: Large Center (LC), Large Edge (LE) and Small (S) (Overall pooled regression: $df_{1,19}$ $F = 0.51$ $p = 0.484$).

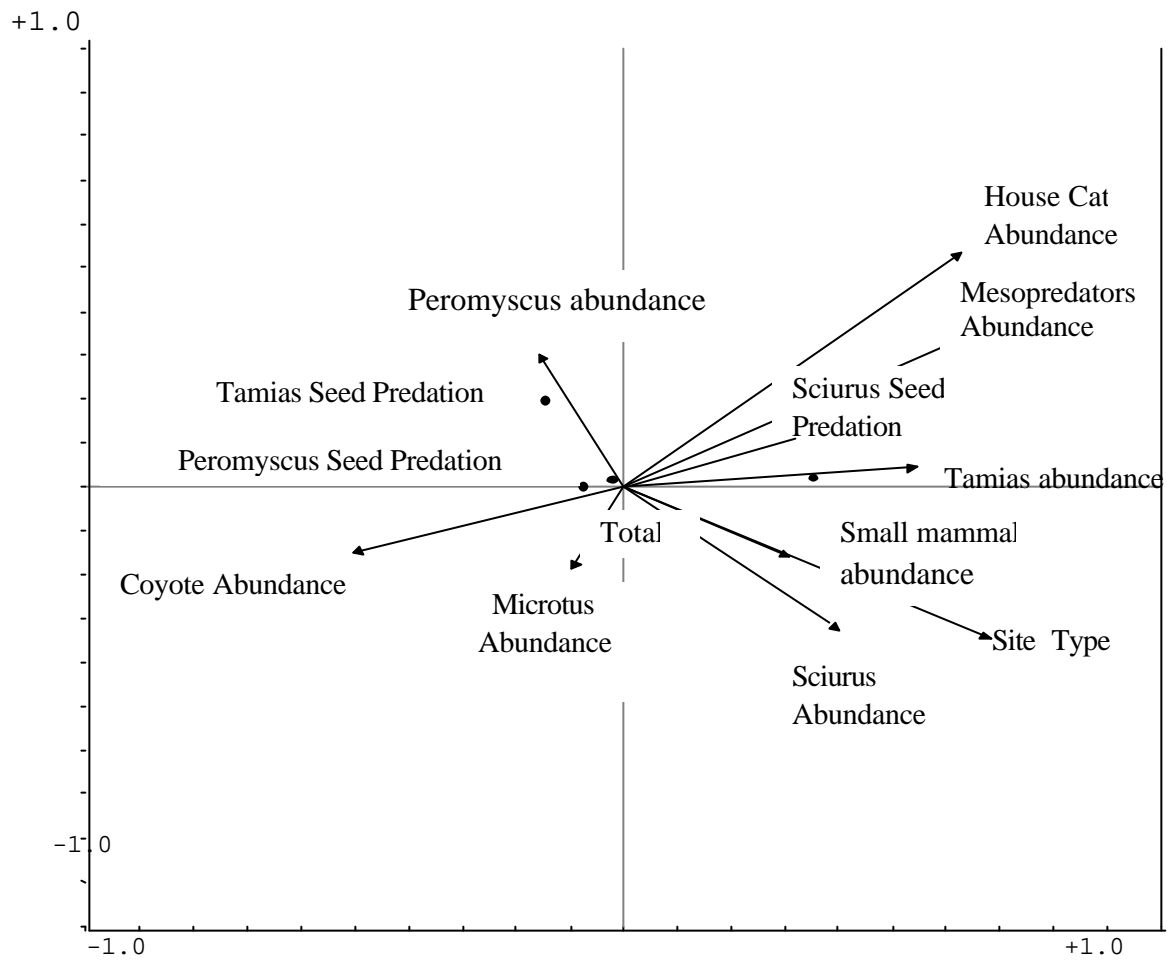


Figure 23a. CCA biplot for pine seed predation and PCA environmental variables. Predation is indicated by proportion of seeds taken by individual species.

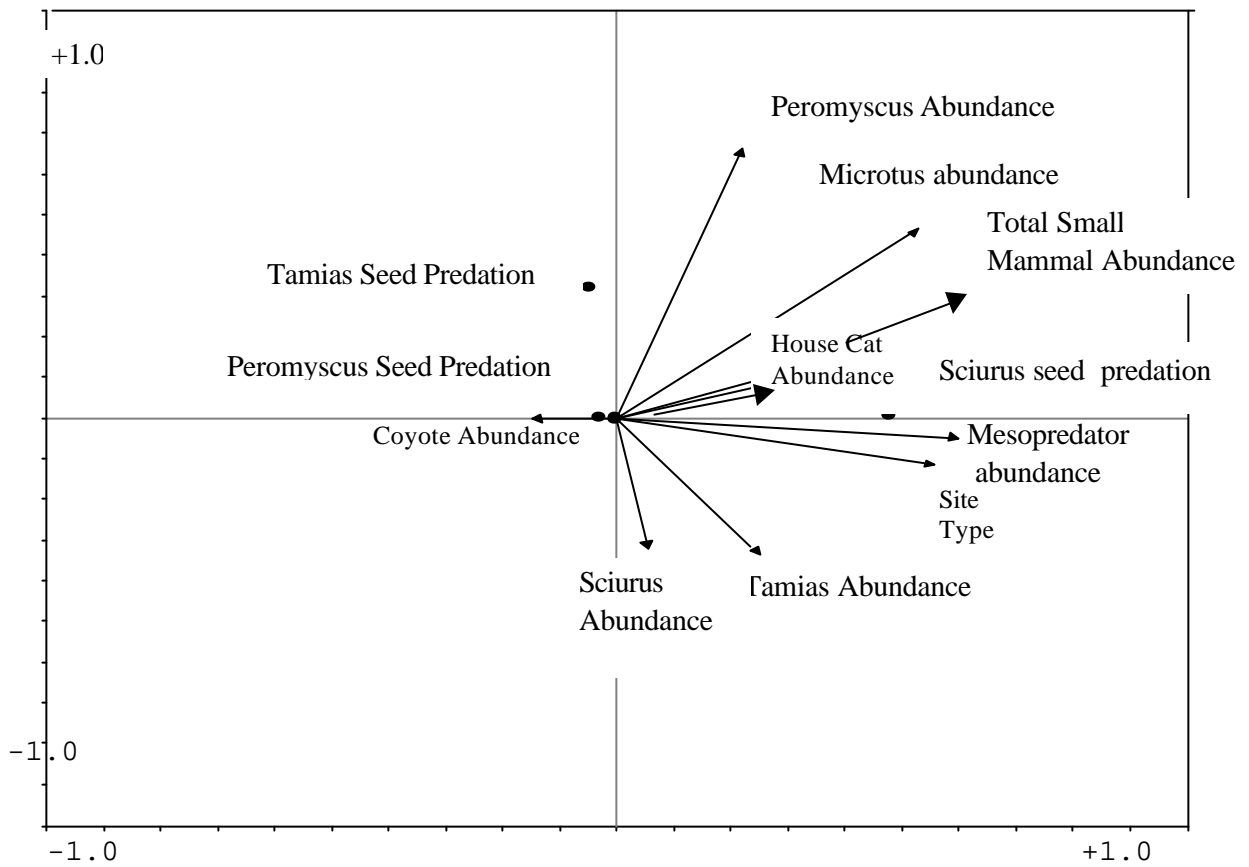


Figure 23b. CCA biplot for lupine seed predation and PCA environmental variables. Predation is indicated by proportion of seeds taken by individual species.

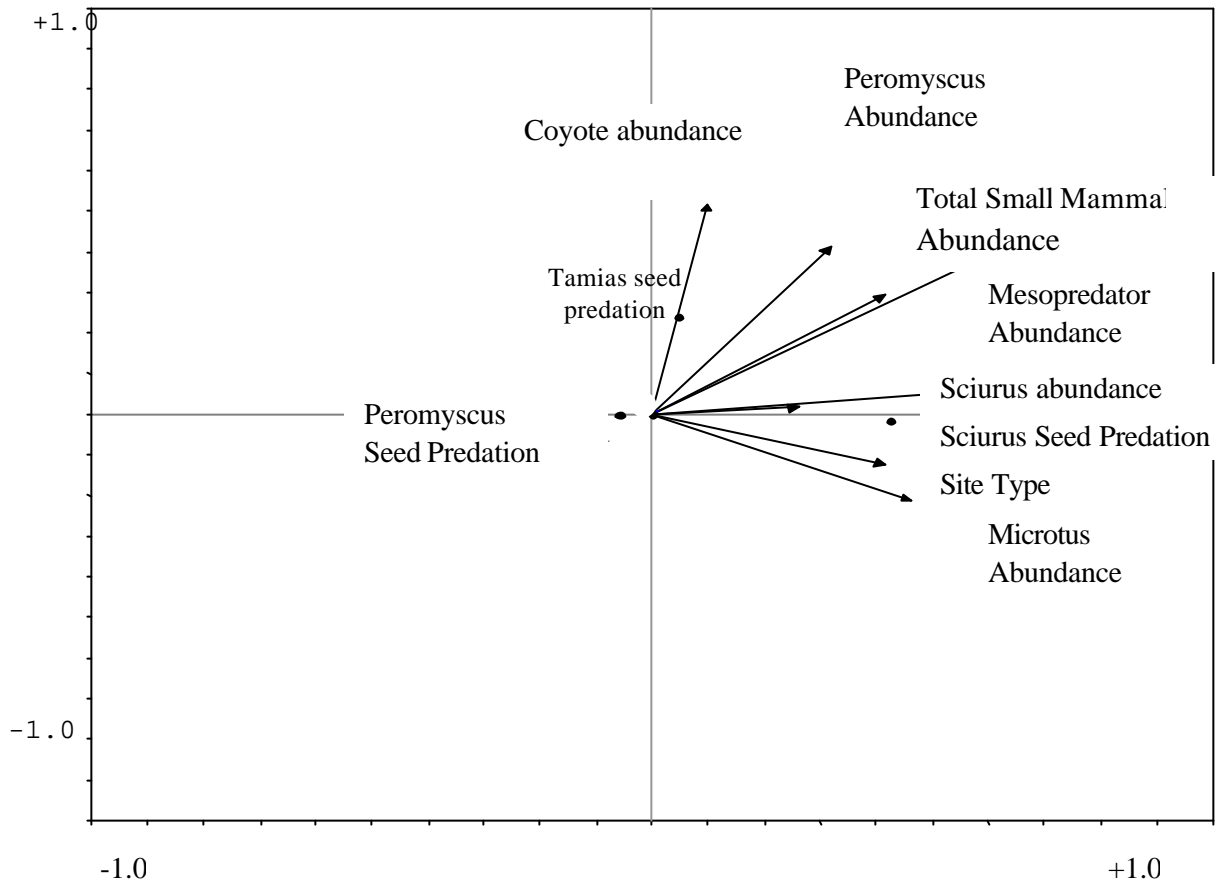


Figure 23c. CCA biplot for New Jersey tea seed predation and PCA environmental variables. Predation is indicated by proportion of seeds taken by individual species.

4 Discussion

Seed predation may play an important role in the regeneration of key plant species in the Albany Pine Bush. I found that *Peromyscus* was the dominant seed predator, which is consistent with previous studies of their role in regulating Plant reproduction, such as in old field succession (Manson 1999, Mittelbach & Gross 1984, Gill & Marks 1991, Ostfeld et al. 1997). Additionally, the existence of edge effects was apparent with a higher level of seed predation at the edges of large fragments. However, the response of small mammals to edges was species specific. Although mesopredators appear to respond to coyote activity, their indirect influence on small mammals and seed predation was not clear.

4.1 Species-Area relationships

Species-area curves for continental islands or habitat patches usually have slopes that are smaller than those found in oceanic island studies. These habitat patches exist in a landscape matrix that does not truly isolate remaining forest fragments. The fragments of the Albany Pine Bush do exhibit a positive relationship between small mammal species and area. However, the species pool is small and the majority of small mammals in the APB are extreme habitat generalists that may thrive in a suburban landscape. For example, *Sciurus* are known to utilize bird feeders to supplement their diet.

4.2 The small mammal community

Previous studies of the response of small mammals to habitat edges show enhanced reproduction and higher densities associated with edges in fragmented habitat (reviewed by Lidicker 1999). I expected small mammal abundance to be higher at the edge of large fragments in comparison to the interior. Additionally, I expected abundance to be lower in small fragments because of resource limitation and the lack of interior forest, but this expectation was moderated by uncertainties over trophic relationships.

Although small mammal abundance was generally higher at the edge of large fragments, I suspect that the similarity in abundance across treatments is due to the high number of habitat generalists. The small mammals I sampled were widely distributed and may use the surrounding suburban matrix. Studies of small mammals in rural landscapes have found that the vagility of some species enables them to adapt their home range structure to highly fragmented landscapes (reviewed by Lidicker 1999). *Sciurus*, for example, are highly mobile and thrive in suburban landscapes.

In my study, the response of small mammals to treatment type varied with species. *Peromyscus*, for example, was consistently found in highest abundance at the edge of large fragments. This relationship is consistent with work by Hansson (1995) who found that small mammal species with limited movement ranges demonstrated pronounced edge effects in distribution and survival, while far ranging species moved evenly over larger areas. Thus, edges of large fragments could act as potential refugia where *Peromyscus* can profit from both environments. The species-specific response of small mammals to

habitat edge is similar to a study by Mills (1996) in which edge-related behavior varied among species.

The apparent negative relationship between *Sciurus* and *Peromyscus* may be a function of unmeasured landscape variables. For example, *Peromyscus* is particularly sensitive to vegetation structure. Although all of my study sites were dominated by mixed-woods habitat, shrub cover and density were not measured and unmeasured differences may have influenced species distributions.

There are a number of possible explanations why estimates of the abundance of small mammals from summer sampling was not directly related to fall small mammal abundance. Most importantly, there appeared to be distinct responses to differences in bait. Peanuts are a highly attractive food source and are useful in detecting a wide number of species. However, one squirrel could conceivably visit all of the tubes in a grid, thus inflating the estimates of squirrels for that site. In a remote video experiment, I observed *Sciurus* taking all of the peanuts on one visit to a tube. Although a single *Peromyscus* was observed entering the tube after the bait was removed, complete removal of bait by squirrels might affect the visitation rates of other species. Tubes were placed with the intention of independent sampling for *Peromyscus* home ranges. However, *Sciurus* home ranges are much larger and could be over sampled. Furthermore, if native seeds are not as attractive to *Sciurus*, I would expect a much lower abundance of *Sciurus* for fall sampling. This potential is evident in the strong negative correlation I found between summer and fall sampling of *Sciurus* abundance.

Secondly, seasonal fluctuations in small mammal populations may also be responsible for variability between sampling periods. For example, Adler (1995) found substantial seasonal variation in the habitat preferences of *Microtus* and *Peromyscus*. He suggests that these differences may be due to density fluctuations and subsequent variability in competitive interactions within and between species (reviewed by Manson et al. 1999).

4.3 Higher trophic interactions

The response of both coyotes and mesopredators to fragmentation was similar to those documented by Crooks & Soulé (1999) in a highly fragmented Southern California habitat. Coyotes were consistently active in large fragments while higher numbers of mesopredators were recorded in small fragments. However, there was limited evidence that carnivore activity affected small mammal abundance in these sites. Similarly, Soulé et al. (1992) found no “coyote effect” evident for small mammals in their study of the impacts of habitat fragmentation on chaparral plants and vertebrates. One reason why this relationship may be difficult to detect is because the small mammal community as a whole does not seem to be sensitive to differences in site type and their reproductive rates may compensate for predation. Most small mammal species are generalists with regard to habitat selection (Hansson 1995). On the other hand, coyotes are known to prey on *Peromyscus* and *Microtus*, so a positive effect of coyote presence on small mammals in this community may be unlikely. Additionally, raptors may play an important role in regulating small mammal populations. Norrdahl and Korpimaeki (1995) found that the presence of raptors had a significant impact on short term population dynamics of voles and shrews. Future studies on the Albany Pine Bush food web should include raptors as a potential regulating mechanism of small mammal populations. Finally, this study was

conducted during one field season. Long term studies are needed to assess adequately the influence of carnivores on other response variables in the ecosystem.

4.4 Seed Predation

4.4.1 Seed Preferences

The results of my study indicate that seed predation may play a very important role in limiting regeneration of pitch pine, blue lupine and New Jersey tea. Although predation of pine seeds is well documented in other ecological communities (Plucinski & Hunter 2001; Nystrand & Granstroem 2000; Ostfeld et al. 1997), the role of granivory on regeneration in pine barrens like the Albany Pine Bush has not been examined. While I found an obvious preference for pitch pine seeds, lupine seeds were also taken in relatively high proportions. In a study of rodent-limited establishment of a western North American bush lupine, Maron and Simms (2001) found that granivory of lupine seeds substantially reduced lupine seedling recruitment. Additional studies on the impact of granivory on blue lupine establishment should include rodent exclusion experiments to examine lupine seedling recruitment. One surprising result of my experiment was the significant level of predation on New Jersey tea seeds with greater than twenty percent removed in two days at all site types. To my knowledge, no studies have documented seed predation on this shrub, and previous emphasis on fire management may have neglected another important regeneration constraint. Overall, it is obvious that seed predation may be an important consideration for preserve managers when planning restoration efforts.

4.4.2 Seed predation and edge effects

Edge effects in the form of increased seed predation were apparent in large fragments. Although the difference in small mammal abundance across site types was not significant, small mammal occupancy appeared consistently higher at the edge in relation to the interior of large fragments for both summer and fall sampling. Further, *Peromyscus* was the dominant seed predator for all seed species. Therefore, the high abundance of mice at edge sites during fall sampling may be a more significant indicator of the influence of edge on seed predation levels. Gill (1997) found reduced pitch pine seedling survival and growth at the edge of the Albany Pine Bush Preserve and speculated that small mammal herbivory may play an important role. The results of my study indicate that mice may be the limiting factor for pitch pine regeneration at the forest edge. Many studies have found that mice play an important role in plant regeneration (e.g., Manson 1999; Mittelbach & Gross 1984; Gill & Marks 1991). Additionally, Ostfeld et al. (1997) found that forest edges experience the most intense seed predation. A similar relationship between edge and seed predation appears likely in the Albany Pine Bush.

4.4.2 Small Mammal Occupancy and Seed Predation

I predicted that small mammal abundance sampled in the summer, as a measure of background population sizes independent of seed preferences, would be positively correlated with seed predation levels sampled in the fall. The unexpected negative relationship between summer occupancy and fall seed predation could be attributed to a

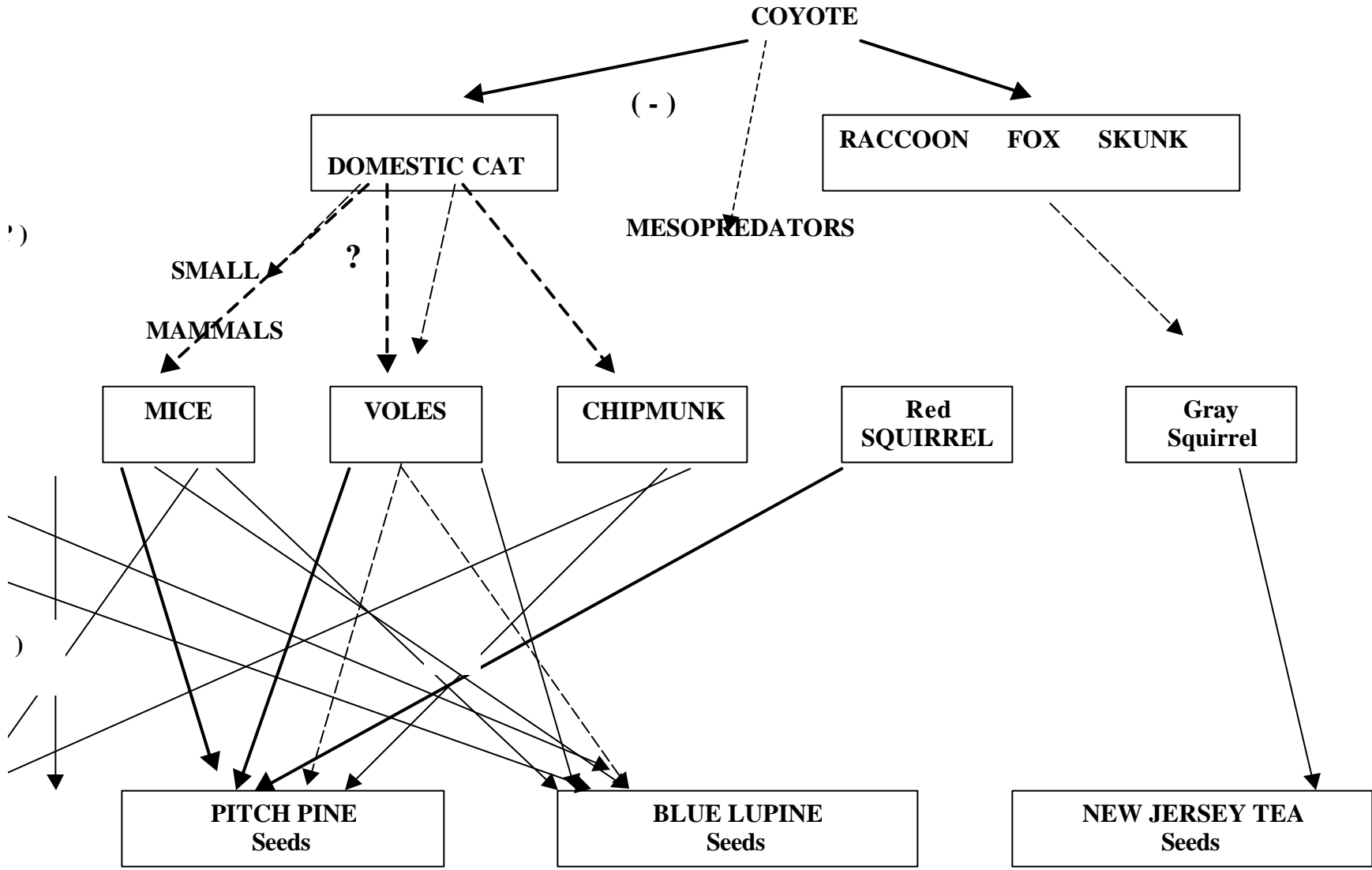
number of possible factors. First, differences in bait used between seasons should have an impact on species detection. This response is most apparent in the strong negative correlation between *Sciurus* occupancy for summer and fall sampling. Secondly, the small mammal community may be responding to differences in carnivore activity during fall sampling. However, mesopredator activity was not monitored during fall sampling so this relationship is unclear. Finally, there may be seasonal differences in the small mammal community that would inhibit a direct linear relationship between summer and fall occupancy.

When I examined my prediction in relation to fall occupancy, small mammal abundance significantly influenced seed predation rates at all site types. This analysis supports the hypothesis that high small mammal activity will influence the intensity of seed predation. Species-specific influences on seed predation were apparent. *Sciurus* exhibited a variable influence on seed predation depending on site type. I interpret this variability to indicate either one of two things. Either 1) Native-seeds are not as attractive to *Sciurus* and will thus under sample actual squirrel densities or 2) *Sciurus* does not play an important role in seed predation on these three plant species in the Albany Pine Bush. To my knowledge, no studies have documented a significant influence of *Sciurus* on the three native seeds species that I have tested. Additionally, the positive correlation between fall occupancy and seed predation for mice is consistent with previous studies that indicate that higher densities of mice will lead to higher levels of seed predation (Ostfeld et al. 1997).

4.5 Trophic Interactions: Missing Links

Prior to conducting this study, we had a limited understanding of food web relationships in the Albany Pine Bush. Although the small mammal community did not respond to the presence of carnivores in the ways I had predicted, the results of my study have filled in a few unknown links in our diagram of possible trophic interactions (Fig. 24). For example, I found that small mammals in the Albany Pine Bush prey on pitch pine, blue lupine, and New Jersey tea seeds and that this predation is enhanced by edge effects. Furthermore, differences in carnivore activity suggest that coyotes inhibit mesopredators in large fragments. In addition, many aspects of this project are ongoing and other researchers continue to develop a fuller picture of the Albany Pine Bush food webs.

Although the results of my study did not suggest the presence of coyote-mediated trophic cascades, the existence of terrestrial trophic cascades may be difficult to detect. A review by Schmitz et al. (2000) found that trophic cascades may be the exception rather than the rule. Terrestrial food webs are inherently complex, and species in these systems are responding to a highly interconnected network of interactions (Schmitz et al. 2000). In addition, there are other landscape variables, like vegetation structure and /or limited resources, that would affect these mammal communities. Therefore, food webs are not only inherently complex but complex landscapes make them even less predictable.



interactions in the Albany Pine Bush. Dotted arrows = unknown

5 Conclusions

Evaluating how habitat fragmentation may affect edge effects and mammal populations is important for understanding complex ecological interactions in remaining habitat fragments. This information is critical for preserve managers to plan restoration efforts and determine management plans for wildlife. Although the presence of coyotes may influence trophic interactions in the Albany Pine Bush, the relationship among carnivores, small mammal abundance and seed predation is not clear. However, the results of my study suggest that seed predation may play an important role in limiting regeneration of key plant species. Furthermore, these effects are exacerbated by high perimeter-area ratios and subsequent edge effects, where seed predators are numerous. It is therefore critical that preserve managers consider the role of small mammals when planning restoration efforts for the successful regeneration and viability of pitch pine, blue lupine and New Jersey tea. Additionally, land acquisition of additional Albany Pine Bush fragments should continue to focus on reducing the overall perimeter-area ratio of the preserve. Finally, long-term studies are needed to gain a better understanding whether carnivore mediated trophic cascades might influence the small mammal and plant community. Evaluating trophic responses over multiple seasons may also provide useful insights on how to manage coyotes in this complex landscape.

Literature Cited

- Abrams, PA. 1996. In: Food webs in Theory and Practice, eds. Polis, G & Winemiller, K. Chapman Hall. New York. pp 113-121.
- Adler, GH. 1995. Habitat relations within lowland grassland rodent communities in Taiwan. *Journal of Zoology* : proceedings of the Zoological Society of London. 237: 563
- Albany Pine Bush Preserve Commission. 1991. Draft management plan and draft of environmental impact statement for the Albany Pine Bush Preserve. Environmental Design and Research, Syracuse, New York, USA.
- Albany Pine Bush Preserve Commission. 1995. Albany Pine Bush Preserve: draft protection and project review implementation guidelines. Albany Pine Bush Preserve Commission, Albany, New York, USA.
- Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71: 355-366.
- Andren, H. 1995. Effects of landscape composition on predation rates at habitat edges. In: *Mosaic landscapes and ecological processes*, eds. by L. Hansson, L. Fahrig and G Merriam. Chapman and Hall, New York. pp. 225-255.

- Bayne, EM & KA Hobson. 1998. The effects of habitat fragmentation by forestry and agriculture on the abundance of small mammals in the southern boreal mixedwood forest. *Canadian Journal of Zoology* 76: 62-69.
- Beckerman, AP, M Uriarte & OJ Schmitz. 1997. Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain. *Proceedings of the National Academy of Science* 94: 10735-10738.
- Crooks, KR & ME Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* 400: 563-566.
- Fletcher, JD, LA Shipley, WJ McShea, & DL Shumway. 2001. Wildlife herbivory and rare plants: the effects of white-tailed deer, rodents, and insects on growth and survival of Turk's cap lily. *Biological Conservation* 101: 229-238.
- Gill, DS & PL Marks. 1991. Tree and shrub seedling colonization of old fields in central New York. *Ecological Monographs* 61: 183-206.
- Gill, R. 1997. The influences of habitat fragmentation on edge effects in the Albany Pine Bush. M.S. thesis. SUNY Albany, Albany, New York.
- Glennon, MJ, WF Porter, CL Demers. 2002. An alternative field technique for estimating diversity of small-mammal populations. *Journal of Mammalogy* In press.
- Gill, RJ. 1997. The influences of habitat fragmentation on edge effects in the Albany Pine Bush Preserve. M.S. thesis State University of New York at Albany.
- Gutierrez, Gutiérrez, J.R., P.L. Meserve, S. Herrera, L.C. Contreras & F.M. Jaksic. 1997. Effects of small mammals and vertebrate predators on vegetation in the Chilean semiarid zone. *Oecologia* 109: 398-406.
- Gomper, ME. 2002. Top carnivores in the suburbs? Ecological conservation issues raised by colonization of North-eastern America by coyotes. *BioScience* 52:185-192.
- Hansson, L. 1995. Local hot spots and their edge effects: small mammals in oak-hazel woodland. *Oikos* 81: 55-62
- Harper, JL. 1977. *The population biology of plants*. Academic press, London.
- Heske, EJ. 1995. Mammalian abundances on forest-farm edges versus forest interior in southern Illinois: is there an edge effect? *Journal of Mammalogy* 76: 562-568.
- Holt, RD. Trophic cascades in terrestrial ecosystems. 2000. *Reflections on Polis et al. Trends in Ecology and Evolution* 15: 444-445.
- Janzen, DH. 1971. Seed predation by animals. *Annual Review of Ecology and Systematics* 2:465-492.

- Kenaly, CP. 2002. Domestic cat predation at the interface of a *Spartina* saltmarsh. Poster: Northeast natural history conference.
- Krebs, CJ. 1994. *Ecology: The experimental analysis of distribution and abundance*. Harpers Collins. New York, New York.
- Lidicker, WZ. 1999. Responses of mammals to habitat edges: an overview. *Landscape Ecology* 14: 333-343.
- Lindenmayer, DB, RB Cunningham, ML Pope. 1999. A large-scale “experiment” to examine the effects of landscape context and habitat fragmentation on mammals. *Biological Conservation* 88:387-403.
- LoGiudice, K, RS Ostfeld. 2002. Interactions between mammals and trees: predation on mammal-dispersed seeds and the effect of ambient food. *Oecologia* 130: 420-425.
- Manson, RH, RS Ostfeld & CD Canham. 1999. Responses of a small mammal community to heterogeneity along forest-old-field-edges. *Landscape Ecology* 14: 355-367.
- MacArthur, RH & EO Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ.
- Manson, RH. 1999. Plant-herbivore interactions along forest edges: clarifying the role of herbivory by small mammals in tree invasion dynamics in old fields. Dissertation. Rutgers University, New Brunswick, New Jersey, USA.
- Maron, JL & EL Simms. 2001. Rodent-limited establishment of bush lupine: field experiments on the cumulative effect of granivory. *Journal of Ecology* 89: 578-588.
- McLaren, BE & RO Peterson. 1994. Wolves, moose, and tree rings on Isle Royale. *Science* 266:1555-1558.
- Menge, BA. 1998. Indirect effects in marine rocky intertidal interactions webs: patterns and importance. *Ecological Monographs* 65:21-74.
- Mills, LS. 1996. Fragmentation of a natural area: dynamics of isolation for small mammals on forest remnants. In: *National Parks and Protected Areas: Their role in environmental protection*. ed. RG Wright. Blackwell Sci Publications Cambridge, MA pp. 199-218
- Mittelbach, GG & KL Gross. 1984. Experimental studies of seed predation in old fields. *Oecologia* 65: 7-13.
- Murcia, C. 1995. Edge effects in fragmented forests: Implications for Conservation. *Trends in Ecology and Evolution* 10: 58-62.

- Norrdahl, K & E Korpimäe. 1995. Effects of predator removal on vertebrate prey populations: Birds of prey and small mammals. *Oecologia*: 103: 241-248
- Nystrand, O & A Granström. 2000. Predation on *Pinus sylvestris* seeds and juvenile seedlings in Swedish boreal forest in relation to stand disturbance by logging. *Journal of Applied Ecology* 37: 449-463.
- Oehler, JD & JA Litvaitis. 1996. The role of spatial scale in understanding responses of medium-sized carnivores to forest fragmentation. *Canadian Journal of Zoology* 74: 2070-2079.
- Ostfeld, RS, RH Manson, CD Canham. 1997. Effects of rodents on survival of tree seeds and seedlings invading old fields. *Ecology* 78:1531-1542.
- Pace, ML, JJ Cole, SR Carpenter & JF Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution* 14: 483-488.
- Palmer, M. 2002. Ordination Methods for Ecologists.
<http://www.okstate.edu/artsci/botany/ordinate/>
- Plucinski, KE & ML Hunter. 2001. Spatial and temporal patterns of seed predation on three tree species in an oak-pine forest. *Ecography* 24: 309-317
- Reschke, C. 1990. Ecological communities of New York state. New York Natural Heritage Program, NYS Department of Environmental Conservation Latham, NY.
- Ritner, D. 1975. Pine Bush: Albany's Last Frontier. Pine Bush Historic Preservation Project. Albany, NY.
- Robinson, GR, RD Holt, MS Gaines, SP Hamburg, ML Johnson, HS Fitch, EA Martinko. 1992. Diverse and contrasting effects of habitat fragmentation. *Science* 257:525-526.
- Rosenblatt, DL, EJ Heske, SL Nelson, DM Barber, MA Miller & Bruce MacAllister. 1999. Forest fragments in east-central Illinois: Islands or habitat patches for mammals?. *American Midland Naturalist* 141:115-123.
- Schmitz, OJ, PA Hambäck & AP Beckerman. 2000. Trophic Cascades in Terrestrial Systems: A review of the Effects of Carnivore Removal on Plants. *American Naturalist* 155:141-153.
- Schoener, TW. 1993. On the relative importance of direct vs. indirect effects in ecological communities. pp 365-411 In: H. Kwanabe, JE Cohen & K Iwaskai eds. *Mutualism and community organization: behavioral, theoretical, and food-web approaches*. Oxford University Press, Oxford.

- Sih, AP, P Crowley, M McPeck, J Petranka & K. Strohmeier. 1985. Predation, competition and prey communities: a review of field experiments. *Annual Review of Ecology and Systematics* 16:269-311.
- Silva, M. 2001. Abundance, diversity, and community structure of small mammals in forest fragments in Prince Edward Island National Park, Canada. *Canadian Journal of Zoology* 79:2063-2071.
- Soulé, ME, D.T. Bolger, A.C. Alberts, R.M. Sauvajot, J. Wright, M. Sorice, and S. Hill. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conservation Biology* 2:75-92.
- Temple, SA & JR Cary. 1988. Modelling dynamics of habitat interior bird populations in fragmented landscapes.
- Ter Braak, CJF & P. Smilauer. 1998. *Canoco reference manual and user's guide to Canoco*. Center for Biometry, Wageningen, Netherlands.
- Terborgh, J & SJ Wright. 1994. Effects of mammalian herbivores on plant recruitment in two neotropical forests. *Ecology* 75: 1829-1833.
- The Nature Conservancy. 2002. Welcome to the Albany Pine Bush. <http://nature.org/wherewework/northamerica/states/newyork/eastern/preserves/art1519.html>.
- Woodroffe, R & JR Ginsburg. 1998. Edge effects and extinction of populations inside protected areas. *Science* 280: 2126-2128.
- Yahner, RH. 1988. Changes in wildlife communities near edges. *Conservation Biology* 2: 333-339.
- Zantopp, K. 2000. History of land use and protection in the Albany Pine Bush. M.S. thesis. SUNY Albany, Albany, New York.
- Zaremba, RE, DM Hunt & AN Lester. 1991. Albany Pine Bush fire management plan: report to the Albany Pine Bush Commission. The Nature Conservancy, New York Field Office, Albany, New York, USA.

Appendix A. Description of the track tube survey method developed by Glennon (2002)

Tubes

Tubes are constructed from rain gutter cut into 12 in sections and taped on one side with duct tape (Appendix 2). Taping on one side allows the tubes to be stacked and easily carried in the field. The lipped sides of gutter were on the same side (top and bottom) and could be interlocked to close the other side of the tube. Using rain gutter for tube construction allows animals up to and including the size of a grey squirrel to effectively enter the tube and leave prints.

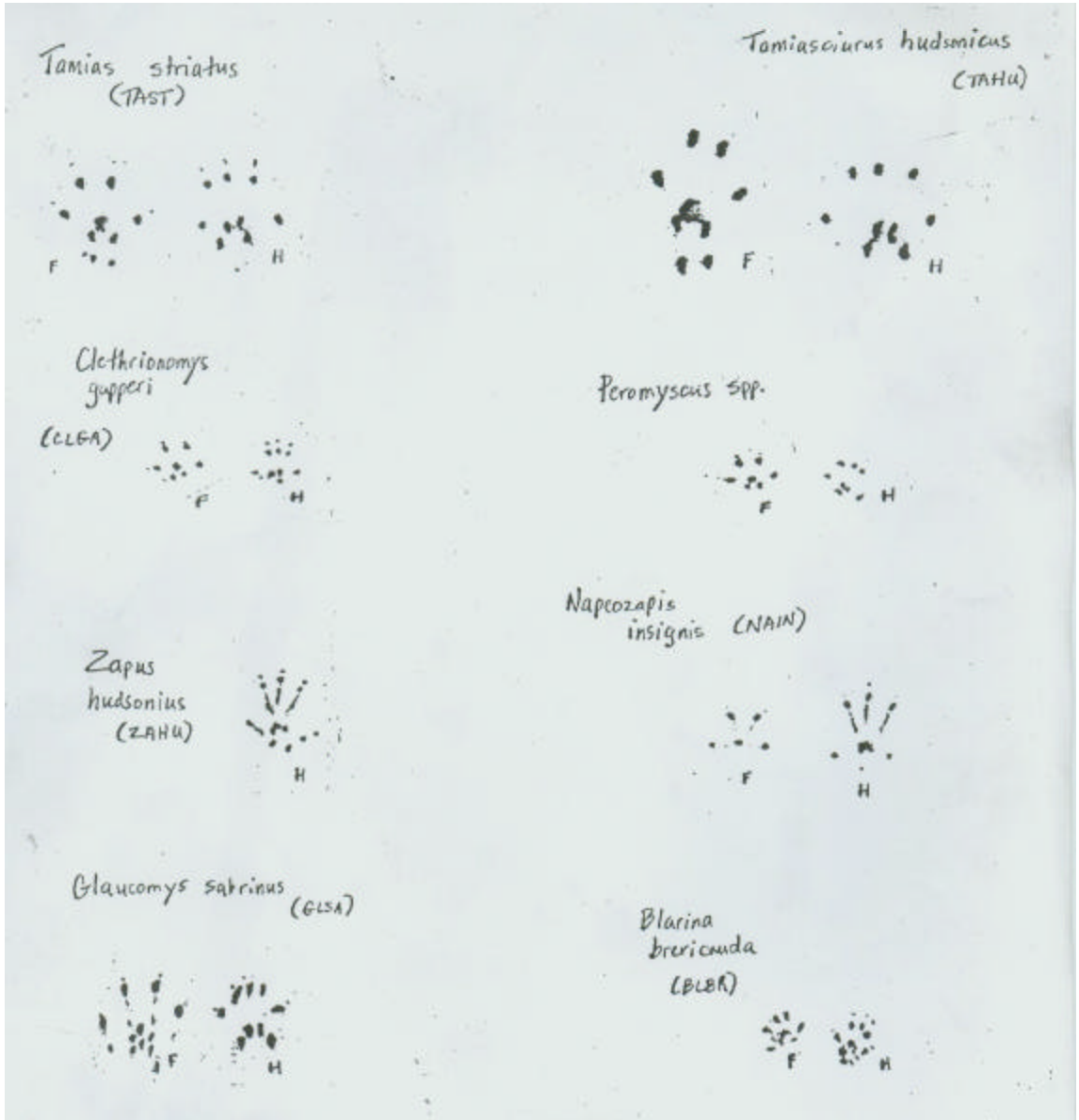
Track Plates

Track plates provide the tracking surface inside of the tubes. Track plates were constructed from aluminum flashing cut into strips 12 in L x 3 in W. Clear contact paper, sticky side up, is attached to each plate. This provides a good tracking surface and can be attached to white paper for a permanent record of tracks. The contact paper protectant is left on each plate until employed in the field. Cloth felt is cut into square pieces, 2.5 x 2.5 in, covered with black ink, and stuck directly onto contact paper on both sides of the plate. After the protectant is removed, track plates are placed inside the tubes with bait in the center of the plate. Animals will then walk on the ink-pads to get to the bait, leaving prints on contact paper inside the tube. When collecting the track plates in the field, ink pads are pulled off and a strip of white paper is attached to the contact paper. Date, study site, and position in the grid is recorded on each strip. Contact paper is then pulled off the track plate and serves as the permanent record of tracks from each tube.

Ink

The ink is made from carbon powder (carbon lampblack or lampblack) and light mineral oil. A ratio of 1:1 carbon black: light mineral oil was used to make ink. Rubber gloves and a mask should be used to make mixtures.

Appendix B. Small mammal print guide from Glennon (2002).



Appendix C. List of small mammal taxa identified in the Albany Pine Bush. *Peromyscus* spp. are indistinguishable in this region

<u>Species</u>	<u>Common Name</u>	<u>Code</u>
<i>Blarina brevicauda</i>	Short-tailed shrew	<i>Blarina</i>
<i>Glaucomys sabrinus</i>	Flying squirrel	<i>Glaucomys</i>
<i>Microtus pennsylvanicus</i>	Meadow vole	<i>Microtus</i>
<i>Napeozapus insignis</i>	Woodland jumping mouse	<i>Napeozapus</i>
<i>Peromyscus maniculaus</i> / <i>Peromyscus leucopus</i>	Deer /White-footed mouse	<i>Peromyscus</i>
<i>Sciurus carolinensis</i>	Gray squirrel	<i>Sciurus</i>
<i>Tamias striatus</i>	Chipmunk	<i>Tamias</i>
<i>Tamiasciurus hudsonicus</i>	Red Squirrel	<i>Tamiasciurus</i>