

The influence of urbanization, patch size, and habitat type on small mammal communities in the New York Metropolitan Region

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Final Report

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Executive Summary

- In 2004, WildMetro originated and organized a study to assess small mammal distribution, abundance, and diversity in the New York Metropolitan Region. During 2004 and 2005, WildMetro conducted small mammal surveys in cooperation with a number of different agencies, including the National Park Service, Marshlands Conservancy, Black Rock Forest, and NYC Parks Department.
- WildMetro conducted a total of 24 small mammal surveys at 12 different urban, suburban, and rural sites from 29 May to 26 October in 2004 and 16 July to 15 November in 2005. We surveyed small mammal communities using capture-mark-recapture methods with arrays of 49 Sherman live traps deployed during 4-day (3-night) trapping periods in forest, salt marsh, shrubland, and grassland sites.
- Individuals from 7 species were trapped during the study: white-footed mouse (*Peromyscus leucopus*), meadow vole (*Microtus pennsylvanicus*), Norway rat (*Rattus norvegicus*), northern short-tailed shrew (*Blarina brevicauda*), least shrew (*Cryptotis parva*), southern red-backed vole (*Clethrionomys gapperi*), and southern flying squirrel (*Glaucomys volans*).
- We found clear differences between small mammal communities in different habitat types, as *P. leucopus* and to a lesser degree *B. brevicauda* were most common in forests, *P. leucopus* was most common in shrublands, *P. leucopus* and *M. pennsylvanicus* were most common in grasslands, and *M. pennsylvanicus* and *R. norvegicus* were most common in salt marshes.
- *P. leucopus* was by the far the most abundant species in forests, grasslands, and shrublands, and the species was present at higher densities in sites with denser and more complex understory vegetation.
- Salt marshes had significantly higher small mammal diversity than all other habitats, and while densities of individual species varied widely between habitat types, overall small mammal density was not significantly different between any of the habitat types.
- Deer density negatively correlated with small mammal density in forests, and patch size also negatively correlated with small mammal density in forests. Small urban patches are therefore likely to have substantially higher small mammal densities than large patches, but it is unclear whether such high densities are desirable from a conservation and human health perspective.
- Urbanization, patch size, and deer density did not significantly influence small mammal diversity in forests, indicating that small, urban green spaces can support small mammal communities mostly representative of the region as a whole.
- Our trapping protocol probably under-represented insectivorous species such as shrews, and our results may not be pertinent for these types of species (particularly those at low density). Future methods will incorporate pitfall traps to obtain more accurate data on all small mammal species at survey sites.

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Introduction

The New York Metropolitan region, an area that includes parts of New Jersey, Connecticut, and New York State, is one of the most urbanized and densely populated areas in the world. Urban zones have traditionally been characterized as harsh, patchy, and biologically sparse, with little value to conservation or ecological research. The scientific community is increasingly altering this perception, however, and coming to view urban zones as biologically important and valuable for research (McDonnell *et al.* 1997; Pickett *et al.* 2001). The New York Metropolitan region includes natural areas that contain a variety of plants and animals that have adapted to urban ecosystems. These green areas are distributed in various patch sizes along an urban gradient extending from the city center to the surrounding suburban and rural landscape, which makes them excellent areas for pursuing ecological research (Kunick 1982; Cousins 1982; Goldstein-Golding 1991; Sauvajot *et al.* 1998).

Small mammal communities may be particularly important in elucidating the effects of urbanization on biological systems. Rodents and shrews can play a key role in influencing the biodiversity of urban green spaces by shaping successional dynamics and future composition of vegetative habitats (Pusenius *et al.* 2000; Hollander and Vander Wall 2004). They can have a strong influence on the presence or absence of a wide array of wildlife either through competitive interactions (Morin 1999; Eccard and Ylönen 2003; Francl *et al.* 2004) or by serving as the prey base for carnivorous species, which are often of greater conservation concern. Furthermore, small mammals may be good indicators of habitat quality and landscape-level conservation threats, as high small mammal densities are often associated with superior habitat quality (Ostfeld *et al.* 1985; Krohne and Hoch 1999; Carey and Harrington 2001). Small mammals also have important implications for human health, since many diseases (including bubonic plague, hantavirus, and lyme disease) are strongly associated with them (Donahue *et al.* 1987; Childs *et al.* 1994; Mills and Childs 1998; Keeling and Gilligan 2000; Ostfeld and Keesing 2000).

Despite their potential usefulness as models, small mammal communities associated with habitat types native to the New York Metropolitan region have not been closely examined. Previous studies exploring the habitat preferences of small mammals provide us with general expectations of the species we are likely to find in habitats around New York City. White-footed mice (*Peromyscus leucopus*) are commonly considered habitat generalists, and are potential residents of shrubland, forest, and grassland habitat types (Dueser and Shugart 1978; Kaufman *et al.* 1983; Adler and Wilson 1987). Although generalists, white-footed mice are usually found at higher densities in hardwood forest habitat, areas with large volumes of stumps and logs, and areas with dense ground cover (Dueser and Shurgart 1978; Barnum *et al.* 1992; Flowerdew and Ellwood 2001; Brannon 2005). Barnum *et al.* (1992) tracked the path choice of adult *P. leucopus* using fluorescent powder, and found significant preferences for paths near logs greater than 5 cm in diameter, as well as significant decreases in travel as vegetative cover thinned. Among other species commonly found in the New York Metropolitan region, meadow voles (*Microtus pennsylvanicus*) tend to be restricted to grasslands, while short-tailed shrews (*Blarina brevicauda*) and masked shrews (*Sorex cinereus*) favor moist herbaceous and woody habitats (Getz 1961; Howell *et al.* 1984).

In contrast to the small mammal communities of forests and grasslands, less data are available from salt marshes. Small mammals in tidal marshes are generally considered transients, or residents of only the high marsh vegetation, though *M. pennsylvanicus* may nest under salt

marsh grasses year-round (Shure 1971; Shanholtzer 1974; Howell *et al.* 1984). *P. leucopus* have also been recorded in wet areas (Kitchings and Levey 1981), but the extent to which these and other species are present in salt marshes in the New York Metropolitan region is unclear. Cook (1989) reported the presence of Norway rats (*Rattus norvegicus*) and possibly Black rats (*Rattus rattus*) in Jamaica Bay, but he did not identify population sizes or densities for either of these species.

The abundance of *Phragmites* in northeastern salt marshes is a matter of ongoing concern. Though the species' invasion of North American wetlands is relatively recent, it has been highly intensive, and may be driven by human-caused sedimentation, eutrophication, and decreased oxygen levels in marsh waters (Marks *et al.* 1984; Roman *et al.* 1984). Natural area managers have observed the species' rapid spread, as well as its potential to outcompete native vegetation that animals utilize for food resources, habitat, nesting sites, etc., with growing anxiety (Alison Beall, personal communication). In light of these concerns, this study will examine small mammal use of *Phragmites* vegetation, and will also utilize salt marsh habitat's typical division into distinct bands of vegetation to investigate microhabitat associations of small mammals.

General patterns of habitat preference observed in previous studies, however, may not correlate with sites in New York City, since urbanization might exercise a substantial influence on the composition of small mammal communities. Urban habitat patches are likely to be smaller in size, more exposed to invasive species, and surrounded by barriers to dispersal (Mahan and O'Connell 2005). Nonetheless, urban patches of native habitat may still contain the necessary microfeatures to support a robust small mammal community. Dickman and Doncaster (1987), for example, found that small mammal densities in urban areas were most strongly related to vegetation, with animals in urban areas exhibiting habitat preferences nearly identical to conspecifics in non-urban areas. Urban parks may therefore play an important role in preserving the microhabitat features necessary to maintain sizeable populations of native small mammal species with small home range requirements. If urban barriers suppress characteristic dispersal rates, however, urban populations may grow abnormally large (Mahan and O'Connell 2005).

This study was designed to obtain a clearer picture of how urbanization, patch size, habitat type, and other factors affect small mammal communities in the New York Metropolitan region. We used live-trapping surveys to describe and compare the structure of small mammal communities among and between a variety of native habitats such as tidal salt marsh, forest, shrublands, and grasslands; to compare the structure of small mammal communities in urban and rural sites and at different patch sizes; and to collect information that will be useful both for improving the quality of remaining urban habitat and for conserving urban biodiversity. As municipalities continue to expand, maintaining urban natural areas will be critical to ensuring resource sustainability in the future on both local and regional scales (Bengston *et al.* 2004). Gathering baseline data on these areas, and understanding the complex effects that urbanization has on ecological communities, is imperative for managing existing urban biodiversity and for managing biodiversity in ecosystems that may become subject to urban sprawl in the future.

Methods

Study sites

From 2004 to 2005, WildMetro surveyed small mammal communities in a total of 24 trapping arrays at 12 different sites in the New York Metropolitan region. Some sites and arrays

were sampled multiple times over this 2-year period, while others were sampled once. We estimated patch size in hectares (ha) for each site from open access satellite photos provided by GoogleMaps (Google 2005), and considered all paved roads visible from aerial photos and major bodies of water as barriers to dispersal (Oxley *et al.* 1974; Klee *et al.* 2004). All patches were therefore surrounded by paved roads and/or water bodies, but it is possible that thin strips of vegetation penetrated these boundaries and acted as dispersal corridors, effectively increasing patch size. Patch sizes for salt marshes, however, were calculated from only the area of the salt marsh, and adjacent non-marsh vegetation was excluded even if no roads or bodies of water were present. Following Marzluff *et al.* (2001), we classified each site as urban, suburban, or rural (no wildlands sites were sampled; see Appendix III) and obtained deer densities from site managers.

Site	Dates Surveyed	Patch Size (ha)	Urbanization class	Habitat type	Vegetation Description
Hunter's Island (Plot 204)	July 9 – 11, 2004	68	Urban	Forest	Old growth forest
Hunter's Island (Plot 207)	October 23 – 26, 2004	68	Urban	Forest	Old growth forest
New York Botanical Garden	May 13 – 19, 2004	16	Urban	Forest	Old growth forest
New York Botanical Garden	October 2 – 4, 2004	16	Urban	Forest	Old growth forest
New York Botanical Garden	July 16 – 19, 2005	16	Urban	Forest	Old growth forest
New York Botanical Garden	Sep 12 – 17, 2005	16	Urban	Forest	Old growth forest
Pelham Bay Old Oak	June 9 – 13, 2004	43	Urban	Forest	Young (20 yrs) secondary forest
Spring Creek High Marsh	Oct 10, 2005	130	Urban	Shrubland	Mix of <i>Phragmites</i> (10-15'), trees, and woody vegetation
Spring Creek Low Marsh	Oct 16 – 17, 2005	0.35	Urban	Marsh	<i>Spartina alterniflora</i>
Van Cortlandt Park (Plot 310)	July 15 – 16, 2004	87	Urban	Forest	Old (~100 yr) secondary forest
Big Egg High Marsh	Oct 10, 19, 21, 2005	2.1	Suburban	Shrubland	Shrubland/grassland with mix of <i>Phragmites</i> , bayberry shrubs, vines, and grasses
Big Egg Low Marsh	Oct 16 – 20, 2005	2.8	Suburban	Marsh	Shrub forest; <i>M. cerifera</i> shrubs (5')
Floyd Bennett Field Area D	Oct 27 – 29, 2005	3.4	Suburban	Grassland	Low (6") grass
Floyd Bennett Field Area G	Oct 27 – 29, 2005	18	Suburban	Grassland	Low (6") grass
Fort Tilden Edge/Grassland	Nov 13 – 15, 2005	90	Suburban	Grassland	Mosaic of beach grass (1') and shrubs (7')
Fort Tilden Interior/Forest	Nov 13 – 15, 2005	90	Suburban	Forest	Shrub/maritime forest
Marshlands Cons. Forest	Sep 29 – Oct 1, 2005	69	Suburban	Forest	Old (~100 yr) secondary forest
Marshlands Cons. Meadow	Sep 29 – Oct 3, 2005	69	Suburban	Grassland	Mix of vines, shrubs, grass (5')
Marshlands Cons. Salt Marsh	Sep 29 – Oct 1, 2005	69	Suburban	Marsh	<i>Spartina alterniflora</i> , <i>S. patens</i> , <i>Phragmites</i>
Sandy Hook High Marsh	Nov 3 – 5, 2005	1	Suburban	Shrubland	Shrub/maritime forest
Sandy Hook Low Marsh	Nov 3 – 5, 2005	3.5	Suburban	Marsh	<i>Spartina alterniflora</i>
Black Rock Forest (2004 site)	October 17 – 19, 2004	5625	Rural	Forest	Old (~100 yr) secondary forest
Black Rock Forest High Slope	Aug 5 – 9, 2005	5625	Rural	Forest	Old (~100 yr) secondary forest
Black Rock Forest Low Slope	July 24 – 27, 2005	5625	Rural	Forest	Old (~100 yr) secondary forest

Table 1. Location and description of sites surveyed during 2004 and 2005.

Hunter's Island, Pelham Bay Park

Hunter's Island is a 68 ha wildlife sanctuary situated within the 1119 ha Pelham Bay Park. Originally a true island, it was connected to the mainland with dredge material in 1937 (NYC Parks 2001). The site contains old growth forest dominated by tulip trees, oaks, and butternut hickory. We surveyed small mammals at two locations (plots 204 and 207) on Hunter's Island in 2004.

The New York Botanical Garden

The New York Botanical Garden forest is a 16 ha patch of native forest contained within the larger 100 ha New York Botanical Garden (NYBG), which is surrounded by an urban matrix in the Bronx, NY. The forest consists mostly of old growth characterized by maples, black cherry trees, oaks, and black birches. We established a study plot in the forest in 2004, and sampled the site four times – twice in both 2004 and 2005.

Pelham Bay Old Oak

In Pelham Bay Park's Southern Section there is a white oak (*Quercus alba*) estimated to be between 200 and 400 years old. Formerly a wooded savannah, the site is transitioning to secondary forest, though there is still low, grassy vegetation in the area immediately under the oak. We surveyed the site in 2004.

Spring Creek

Northeastern salt marshes are typically characterized by *Spartina alterniflora* grass in the low marsh (i.e., the area of the marsh inundated at high tide), *Spartina patens* in the less-frequently flooded high marsh, and various shrubs, grasses, and invasive *Phragmites australis* reeds in adjacent upland vegetation.

Spring Creek Park, located in northern Jamaica Bay, contains a small (0.35 ha) area of low salt marsh and sandy flats, transitioning to a larger (130 ha) area of maritime shrubland and *Phragmites*-dominated upland vegetation. Material from the dredging of Jamaica Bay channels, together with large amounts of litter, has accumulated in and substantially degraded Spring Creek's vegetative community, leading environmental engineers to propose a restoration project at the site (Burke *et al.* 2004). In 2005 we surveyed almost the entirety of the small intertidal salt marsh, along with an adjacent area of mixed woods and *Phragmites*-dominated shrubland, for small mammals.

Van Cortlandt Park

Van Cortlandt Park is a New York City park encompassing 464 ha. We surveyed a site in 2004 in the Northwest Forest, a secondary forest last logged about 100 years ago. The site is characterized by mixed hardwood forest of tulip poplars, white ash, and oaks (McDonnell *et al.* 1990).

Big Egg

Big Egg Marsh is located on the eastern side of Jamaica Bay and contains relatively large areas of intact salt marsh in addition to a smaller salt marsh recently restored by the National Park Service (NPS) (total salt marsh area is approximately 2.8 ha). This restoration project utilized the technique of "thin-layering," where dredged slurry is sprayed onto tidal marshes to raise their elevation and reestablish salt marsh vegetation, followed by the hand-planting of *Spartina alterniflora* seed (Frame and Adamo 2004). In 2005, we surveyed the restored salt

marsh area and an adjacent area of upland vegetation containing mixed *Phragmites* reeds, some woody vegetation, bayberry (*Myrica cerifera*) shrubs, vines of poison ivy (*Toxicodendron radicans*), and grasses such as *S. patens*, *Distichlis spicata*, *Limonium latifolium*, *Juncus Canadensis*.

Floyd Bennett Field

Floyd Bennett Field operated as an airfield under various agencies from its opening in 1931 until its closing and transfer of management to NPS in 1972. Formerly a series of marsh islands, the site was filled with dredge soil and joined to Brooklyn as the airfield was built (Elbin and Koontz 1998). Grasslands at the site (collectively termed Grassland Restoration and Management Project – GRAMP – areas) are managed under a mowing regime designed to maintain grassland cover for native bird species. At the time of our survey (late October 2005), the fields had been mowed about two months earlier, and grasses were approximately 6” tall. The network of asphalt runways and roads remains, separating the vegetated areas into discrete patches. We conducted small mammal surveys in two of these GRAMP grassland patches: Area D (approximately 3.5 ha) and Area G (approximately 18 ha).

Fort Tilden

Fort Tilden, located on the western end of Rockaway Peninsula, is a former military site now part of Gateway National Recreation Area that retains substantial natural areas. In particular, the 90 ha Back Fort area of Fort Tilden contains older maritime forest vegetation uncommon in other protected areas and parks in the New York Metropolitan Region. We surveyed two locations within the Back Fort in 2005: one grassland area near the southern beach containing shrubs, low trees, and beach grass vegetation, and a second site in an interior, forested area.

Marshlands Conservancy

Marshlands Conservancy is a 69 ha nature preserve of the Westchester County Department of Parks, Recreation, and Conservation located in suburban Rye, NY. The park contains three different habitat types: older secondary forest, meadow vegetation (structured grassland containing a mix of goldenrods, tall grasses, vines, and some shrubs), and approximately 8 ha of salt marsh (characterized by *S. alterniflora*, *S. patens*, *Distichlis spicata*, *Limonium latifolium*, and *Juncus Canadensis*). We surveyed all of these areas for small mammals in 2005.

Sandy Hook

The Sandy Hook Unit of Gateway National Recreation Area is located on a peninsula that extends northwards from the suburb of Highlands in northeastern New Jersey towards the southern tip of Manhattan. It hosts barrier beaches, a historic lighthouse, and a historic military fort. In 2005, we surveyed the 3.5 ha *S. alterniflora* salt marsh adjacent to Horseshoe Cove and a 1 ha area of contiguous upland vegetation consisting of mixed shrubland and secondary maritime forest.

Black Rock Forest

Black Rock Forest is a privately owned natural area operated by a not-for-profit research consortium of public and private institutions, located approximately 80km north of New York

City in the central portion of the Hudson Highlands near Cornwall, NY. The site contains upland old growth forest, riparian, and small wetland habitats relatively preserved from human exploitation and representative of the dominant regional ecosystem. While the Forest preserve itself contains approximately 1530 ha, it connects to Storm King State Park and other forested areas for an effective patch size of approximately 5600 ha. In 2004, we surveyed one 1-ha plot located on the northern slope of Black Rock Hill; in 2005, we surveyed this site a second time, along with another 1-ha plot low on the slope of Frog Hill adjacent to Hulse Road.

Sampling methods

Small mammal surveys were conducted using a capture-mark-recapture method, commonly used in small mammal research to determine species presence/absence and species diversity, to estimate population size, and to assess the demography of the local population. Our trapping protocol was designed to capture nocturnal and crepuscular, terrestrial (not diurnal, subterranean, or arboreal) species. All trapping periods occurred between May 2004 and November 2005.

We used Sherman live traps (aluminum, 3”x 3”x 9”) in all our surveys. In most sites, arrays were composed of 49 traps placed 15m apart in a 7x7 grid (Burns 2005). This array allows a survey area of approximately 1 hectare, which is typically large enough to contain home ranges of multiple individuals of a variety of small mammal species, such as mice, shrews, and voles. In sites limited in area or with non-linear boundaries (such as salt marshes, which often have extremely curvaceous borders and contain large mudflat areas that are unsafe to directly sample) the trapping array was fitted to the area available. These design adaptations were determined on an individual-site basis, either by changing the trap spacing distance from 15m to 10m and/or by designing irregularly-shaped trapping arrays.

Trapping took place over a five-day session. During the first night, traps were positioned in the grid at the appropriate spacing distance, closed, and left with bait (birdseed and peanuts) scattered externally to allow animals to become familiar with the traps (“prebaiting”). Traps were covered with local vegetation or substrate to keep them inconspicuous. Over the following three nights, traps were internally baited and left open during the night, and checked and closed at dawn. Traps were prebaited or baited and placed in the grid during the two hours before sunset. In some cases, heavy rain or cold overnight temperatures (<40°F) made consecutive trapping nights unfeasible. When trapping was delayed mid-session for two or more days, we added an additional night of prebaiting to re-habituate animals to the traps and to maintain the presence of high-quality food near traps.

We used a modified trapping protocol in salt marshes that allowed us to compare salt marsh and upland habitat. Two separate trapping arrays were surveyed in each salt marsh: one located in low marsh (e.g., dominated by *Spartina alterniflora*) and one in adjacent upland vegetation (either shrubland or forest). The two grids were placed relatively close to one another (<30m apart) to increase the likelihood of recapturing animals from the neighboring grid, which could potentially show individual animal movement between low and high marsh habitats. Because of the similarities between trapping arrays, we considered these adjacent grids as paired samples. The small mammal species we aimed to trap are nocturnal, and the movement of nocturnal species in salt marshes is likely to be highest when low tide occurs during the night. We therefore trapped in salt marshes during nights when low tide occurred between 12am and 4am. Since salt marshes were flooded during the hours surrounding high tide, Sherman traps could not be left overnight either during prebaiting or during a full trapping night. Instead, on

prebaiting nights, bait was scattered at trap locations without traps being put down, and on subsequent trapping nights baited traps were placed in the grid approximately three hours before low tide and checked and removed approximately six hours later.

We used a set procedure to process captured animals. Captured animals were removed from the trap, sexed, weighed, aged, individually marked with numbered ear tags, and promptly released at the capture site. Most captured animals were also photographed before release. Ear-tagging was the preferred method for marking animals in this study, because other techniques (such as bleaches, paints, fur-clipping, etc.) generally require longer handling time and are not detectable from year to year. Identifying individual animals in subsequent years is vital in determining survivorship for different age classes. It is a relatively painless form of permanent marking, and neither restricts the normal activity nor adversely affects the well-being of the animal. In most cases, properly applied metal ear tags do not burden small mammals or increase their vulnerability to injury or predation, and are appropriate for the habits and body form of the species (American Society of Mammalogists ACUC 1998). However, alternate techniques were used in some sites and for some species. According to the preferences of the NYBG administration, all animals captured in the NYBG Forest were marked either by fur-clipping or permanent nontoxic markers (Avery Marks-A-Lot). In addition, captured meadow voles (*Microtus pennsylvanicus*) and Norway rats (*Rattus norvegicus*) were marked with non toxic permanent markers, due to handling difficulty.

We employed a large number of precautions to avoid damaging study sites and to ensure the health and safety of captured animals. We avoided trampling the relatively fragile *Spartina* vegetation in salt marsh sites, and concealed or made traps and trap markings as inconspicuous as possible. Field crew members wore plastic or leather gloves whenever checking traps and handling small mammals. In light rain, we placed wooden roof shingles over the Sherman traps to shield any captured animals from rainfall. Water-repellant polyfil bunting was placed in each trap to provide warmth and bedding material if the overnight temperature was predicted to fall below 65°F, and no trapping was conducted if overnight temperatures were predicted to fall below 40°F. As we found higher mortality when temperatures dropped below 50°F, in October 2005 we adjusted our protocol to begin checking traps and processing animals before dawn. We also processed lethargic animals and sensitive species before others, and did not ear tag shrews, to minimize their handling time and further reduce mortality. Animals that succumbed to trap mortality were preserved in a solution of 70% alcohol, and will be turned over to the appropriate agencies according to previous arrangements.

Data analysis

We used an α value of 0.05 for all statistical tests of significance. All statistical tests are two-tailed unless otherwise indicated and were computed using the StatsDirect program (StatsDirect Ltd 2005).

We computed an estimate of the total population of each species for each trapping survey. We used the CAPTURE program (Otis *et al.* 1978; White *et al.* 1982) to compute population sizes whenever a survey contained 7 or more recaptures of a single species. CAPTURE is widely regarded as a powerful and accurate estimator of true population sizes from capture-mark-recapture data (Rexstad and Burnham 1991). Population sizes were also estimated using the Schnabel population estimate (Schnabel 1938) when we completed at least three nights of trapping and at least one individual of a species was recaptured. Failing either of these conditions, we used the minimum number of animals captured as an estimate of the total

population. The Schnabel population estimate is not as powerful as the CAPTURE model, but it is a more robust estimator of population sizes than minimum number of animals when a substantial number of new individuals are still being captured on the final day of trapping. To account for uncertainty in these tests, the final population estimate that we report in the results, and that we used in statistical calculations, was an average of the two most powerful estimators of total population size. This estimate is therefore either the mean of the results from CAPTURE and Schnabel, the mean of Schnabel and minimum number of animals, or just the minimum number of animals captured when data were not available to compute either Schnabel or CAPTURE population estimates.

To compute small mammal density we used the final population estimate as described above for each species, added the populations for all species from one survey together, and divided by the area surveyed. To estimate the area surveyed, we assumed that each trap caught animals from a 15x15m square centered on the trap. When traps were placed 10m apart, we did not double-count overlapping areas between traps as part of the total area surveyed.

For each survey we also calculated the diversity of the small mammal community. Diversity is a combination of the absolute number of species present (species richness) and the relative abundance of each species (species evenness) in a particular community. We used the Shannon-Weiner diversity index to numerically calculate species diversity for each survey. The Shannon-Wiener index is calculated by the equation

$$H' = - \sum p_i * \ln(p_i)$$

This index is based on the proportional abundance (p_i s) of each species (i) in the total sample of individuals within the community surveyed and emphasizes the more common species in the community. It thereby determines diversity by accounting for both species richness and species evenness. Scores from the Shannon-Wiener index range from a minimum of

$$H'_{\min} = \log(N) * [(N - S + 1) / N] * [\log(N - S + 1)]$$

to a maximum of

$$H'_{\max} = \log_2(S)$$

where S = number of species in the sample (species richness), and N = number of observations. Higher scores indicate greater diversity.

We used one-way ANOVA's to assess overall differences between the four different habitat types (forest, salt marsh, grassland, and shrubland), and we used Tukey's post-hoc test to determine differences between individual habitat types within the ANOVA. Trapping surveys from the same location – even if the trap grids were in different spots – were treated as paired samples. Surveys in salt marshes and surveys in adjacent sites were also treated as paired samples. We used student's t-tests, or paired t-tests when appropriate, to compare differences between two categories.

Deer mice (*Peromyscus maniculatus*) are generally not present in the New York Metropolitan region, and we assumed that all our mice captures represented *P. leucopus* and not *P. maniculatus* as the two species are extremely difficult to differentiate in the field (Burt and Grossenheider 1976; Rich *et al.* 1996; Whitaker 1996; Tessier *et al.* 2004).

Our trap design was based on three assumptions: 1) differences in trap captures represent proportional differences in abundance; 2) capture probabilities remain constant for each trap and during each trapping session; and 3) targeted species will not become trap-weary.

Results

Correlates of habitat type

The twenty-four surveys we conducted showed considerable variation in both density and diversity of small mammals for different sites. Trapping surveys were not all conducted at the same time of year – most of our surveys in 2005 took place during the fall (with the exception of Black Rock Forest and one survey at the New York Botanical Garden) while most of our surveys in 2004 took place in summer – and it is possible that seasonality influenced our results. We observed some seasonal differences in the small mammal community at certain sites, but surveys at these sites took place during different years and it is unclear whether differences were due to yearly fluctuations, seasonal fluctuations, or random chance. In total we sampled 3720 trap-nights (see Table 2; also see Appendix I for species distributions at each site).

Site	Survey date	Habitat type	Total small mammals / ha	Shannon-Weiner Diversity Index	Trap-nights
New York Botanical Garden	May 13 - 19 2004	Forest	109	0.0	280
New York Botanical Garden	Oct 2 -4 2004	Forest	105	0.18	180
New York Botanical Garden	July 16-19 2005	Forest	44	0.0	147
New York Botanical Garden	Sep 12 - 17 2005	Forest	130	0.30	147
Marshlands Cons. Forest	Sep 29 - Oct 1 2005	Forest	1	0.0	147
Black Rock Forest (2004 site)	Oct 17-19 2004	Forest	17	0.82	147
Black Rock Forest Low Slope	July 24-27 2005	Forest	7	0.0	147
Black Rock Forest High Slope	Aug 5 - 9 2005	Forest	8	0.50	147
Pelham Bay Old Oak	June 9-13 2004	Forest	17	0.42	176
Hunter's Island (Plot 207)	Oct 23 - 26 2004	Forest	38	0.0	196
Hunter's Island (Plot 204)	July 9 - 11 2004	Forest	29	0.40	196
Van Cortlandt Park (Plot 310)	July 15 - 16 2004 (incomp.)	Forest	15	0.21	196
Fort Tilden Interior/Forest	Nov 13-15 2005	Forest	59	0.0	147
Marshlands Cons. Meadow	Sep 29 - Oct 3 2005	Grassland	19	0.33	147
Floyd Bennett Field Area D	Oct 27-29 2005	Grassland	0	0.0	147
Floyd Bennett Field Area G	Oct 27-29 2005	Grassland	0	0.0	147
Fort Tilden Edge/Grassland	Nov 13-15 2005	Grassland	93	0.0	147
Spring Creek Low Marsh	Oct 16-17 2005	Salt marsh	7	0.64	76

		(incomplete)			
Marshlands Cons. Salt Marsh	Sep 29 - Oct 1 2005	Salt marsh	4	0.35	151
Big Egg Low Marsh	Oct 16-20 2005	Salt marsh	9	0.50	147
Sandy Hook Low Marsh	Nov 3-5 2005	Salt marsh	20	0.96	135
Spring Creek High Marsh	Oct 10 2005	Shrubland			49
Big Egg High Marsh	(incomplete)		31	0.22	
Big Egg High Marsh	Oct 10,19,21 2005	Shrubland	117	0.0	145
Sandy Hook High Marsh	Nov 3-5 2005	Shrubland	89	0.13	147

Table 2 Small mammal density and community diversity for each of the 24 surveys.

There were no significant differences in small mammal densities between different habitat types (One-way ANOVA, $p > 0.10$; see Figure 1). Differences in diversity, as measured by the Shannon-Weiner diversity index, were, however, significant between the four sampled habitat types (One-way ANOVA, $p < 0.01$; see Figure 2). This difference was almost entirely driven by differences between small mammal communities at salt marshes compared to other habitats. The small mammal communities were significantly more diverse in salt marshes than in forests, grasslands, and shrublands (Tukey's post hoc test, salt marsh vs. grassland $p < 0.01$, salt marsh vs. forest $p < 0.01$, salt marsh vs. shrubland $p < 0.05$), while there were no significant differences in diversity between forest, grassland, and shrubland sites (Tukey's post hoc test, forest vs. grassland $p > 0.10$, forest vs. shrubland $p > 0.10$, grassland vs. shrubland $p > 0.10$). Several species that we captured regularly were restricted to only a subset of the habitat types, however, with Norway rats (*Rattus norvegicus*) being entirely restricted to salt marshes, meadow voles (*Microtus pennsylvanicus*) entirely absent from forests, and short-tailed shrews (*Blarina brevicauda*) restricted to forests. Salt marshes had higher diversity scores largely because species were more evenly distributed in salt marshes than in other habitat types, where *P. leucopus* were by far the most abundant species (see Appendix I). Though we did not have sufficient data to perform a statistical analysis, invasive *Phragmites* reeds did not appear to be strongly linked with reduced small mammal density or diversity, as we captured *M. pennsylvanicus* and *P. leucopus* in *Phragmites* at Spring Creek High Marsh, Big Egg High Marsh, and Marshlands Conservancy.

Figure 1 Small mammal density (# animals per ha \pm SE) in each of the sampled habitat types.

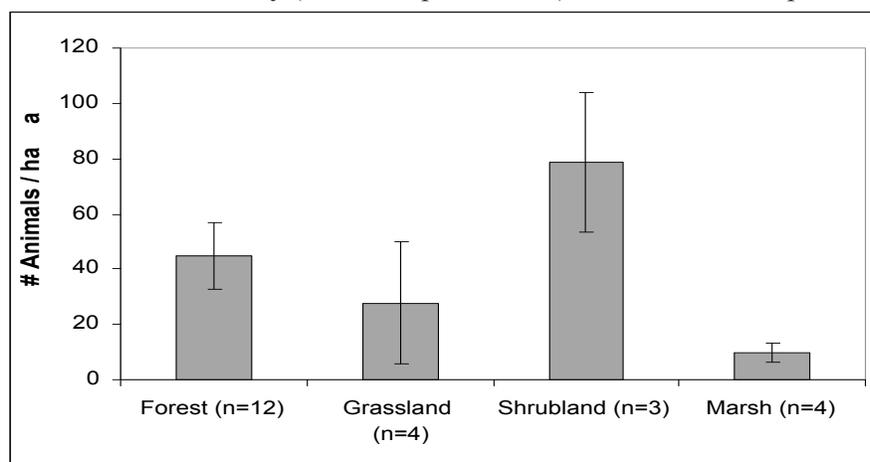
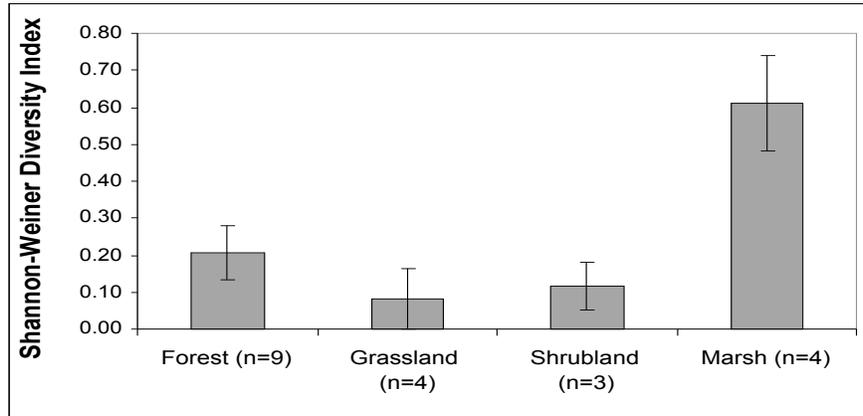


Figure 2 Small mammal diversity (Shannon-Weiner diversity index \pm SE) in each of the sampled habitat types.



In salt marsh areas there were significant differences in the small mammal community between the paired marsh and adjacent sites: salt marsh sites had significantly higher Shannon-Weiner diversity indices than adjacent shrubland or forest sites (Paired t-test, $N=8$, $p<0.05$). There was, however, no corresponding significant difference in overall small mammal density between salt marshes and adjacent sites (Paired t-test, $N=8$, $p>0.10$). Salt marshes also contained different species than adjacent sites. We captured rats in three of the four salt marshes (all except Marshlands Conservancy) and never captured a rat in another habitat. Compared to only adjacent shrubland sites, salt marshes also appeared to contain lower densities of *P. leucopus*, but the difference was not significant (Paired t-test, $N=3$, $p>0.05$, $mean_{shrubland} = 77.8$ mice/ha, $mean_{salt\ marsh} = 1.7$ mice/ha). However, we sampled only three paired sites, and one of the shrubland surveys was incomplete – and hence had an artificially reduced density in our results – suggesting that with more data this difference may be significant.

Differences between small mammal communities in the four different salt marshes were apparent. Although the Shannon-Weiner diversity indices were similar across all four sites, the species that were present varied: meadow voles were found in higher densities at Sandy Hook than in other salt marshes (Fisher’s exact test, $N=4$, $p<0.05$; see Table 3); rats were observed in low densities in Spring Creek, Big Egg, and Sandy Hook salt marshes, and not at all in Marshlands Conservancy, though differences in rat capture rates between sites were not statistically significant (Fisher’s exact test, $N=4$, $p>0.10$). The latter result may be attributed to either rats not being present in Marshlands Conservancy or random chance. There was a significant difference in *R. norvegicus* density between low marsh and adjacent sites (Fisher’s exact test, $N=8$, $p<0.01$), and the species was only observed in low marshes. Notably, all four animals (two *P. leucopus* and two *M. pennsylvanicus*) we captured at Marshlands Conservancy were trapped in *Phragmites* above the tidal zone; we captured no animals in the low marsh.

Site	Shannon-Weiner diversity index	<i>Peromyscus leucopus</i> captured	<i>Rattus norvegicus</i> captured	<i>Microtus pennsylvanicus</i> captured
Marshlands Cons. Salt Marsh [†]	0.69	2	0	2

Spring Creek Low Marsh	0.64	0	2	1
Big Egg Low Marsh	0.50	1	4	0
Sandy Hook Low Marsh	0.96	2	3	7

Table 3 Shannon-Weiner diversity index and number of animals captured for all four salt marsh sites

†All animals were captured in *Phragmites* above the tidal zone

We found some evidence suggesting that individual animals move between low salt marsh and adjacent vegetation at low rates. In 997 trap-nights, an individual animal was captured in two adjacent (<30m apart) grids only once (a *P. leucopus* at Sandy Hook was captured once in shrubland and once in salt marsh), even though all four salt marsh sites had adjacent grids with no apparent dispersal barriers between them.

Correlates of patch size, deer density, and urbanization in forests

As we surveyed small mammals in only four grassland, four salt marsh, and three shrubland sites, we were unable to statistically analyze the effects of patch size, deer density, and urbanization within these three habitat types.

At forest sites, patch size and deer density, when analyzed together in a multiple linear regression, significantly correlated with small mammal density – though neither individual correlation was significant in the same analysis (Multiple linear regression with patch size transformed to log patch size, N=13, overall $p < 0.05$, $R^2 = 0.47$, adjusted $R^2 = 0.36$, log patch size $p < 0.10$, deer density $p > 0.10$). Notably, the survey conducted in July of 2005 at the New York Botanical Garden was an outlier (see Table 2), perhaps because it was the only survey of all 24 where peanuts were not used in the bait. We therefore removed this survey from all subsequent analyses. A re-calculation of the above analysis without this survey indicates no substantive changes (Multiple linear regression with patch size transformed to log patch size, N=12, overall $p < 0.05$, $R^2 = 0.51$, adjusted $R^2 = 0.40$, log patch size $p < 0.10$, deer density $p > 0.10$).

Analyzed individually, the relationships between deer density and small mammal density, and patch size and small mammal density, are clearer; the relationship between urbanization and small mammal density is less so. Deer density had a very strong negative correlation with small mammal density at forested sites (Single linear regression, N=12, exponential model, $p < 0.001$, $R^2 = 0.73$, see Figure 3), and patch size was also negatively correlated with small mammal density (Single linear regression, N=12, $p < 0.05$, $R^2 = 0.62$, see Figure 4). Though we had too few data points to conduct an ANOVA between urban, suburban, and rural sites, there appears to be a positive relationship between increased urbanization and increased small mammal densities in forests. As more urbanized sites were generally smaller and never contained deer, it is unclear whether 1) smaller patch size, 2) reduced deer density, or 3) a third (as of yet unidentified) factor associated with urbanization may have caused the higher small mammal densities generally found in urban forests.

Figure 3 Deer density and small mammal density at forest sites.

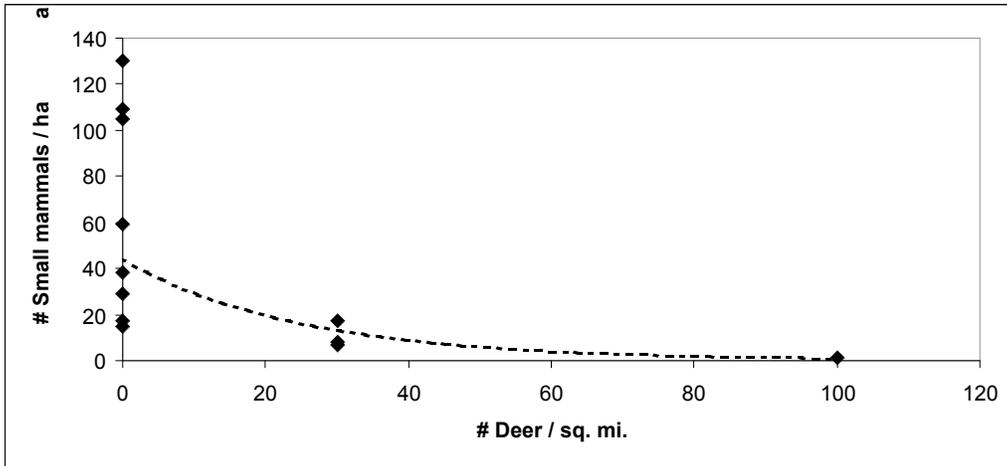


Figure 4 Patch size and small mammal density at forest sites.

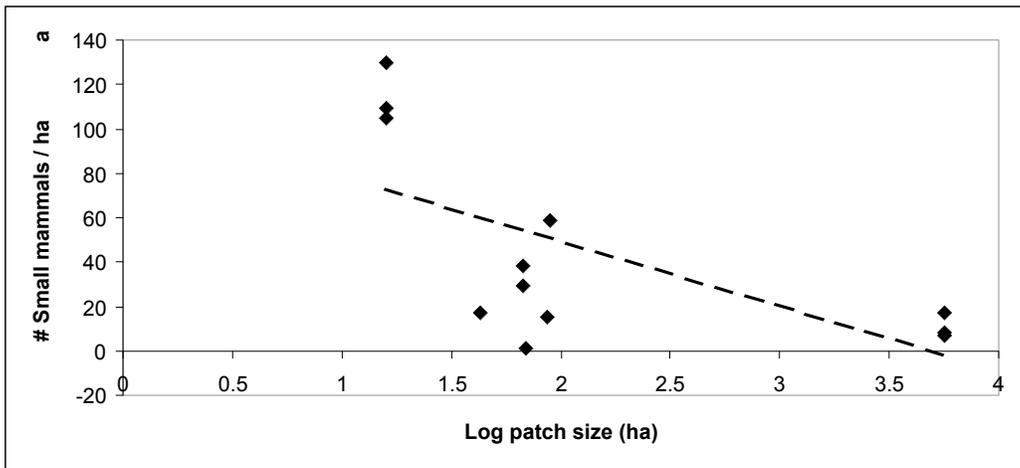
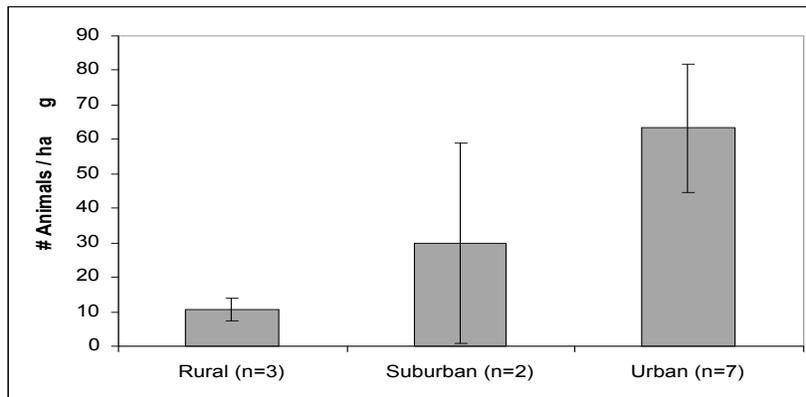


Figure 5 Urbanization and small mammal density at forest sites.



In contrast to these results, patch size and deer density were not significantly correlated with small mammal diversity in forest sites (Multiple linear regression with patch size transformed to Log patch size, N=12, overall $p>0.10$, $R^2=0.30$, adjusted $R^2=0.15$, Log patch size $p<0.10$, deer density $p>0.10$). There was no relationship between patch size and diversity (N=12, $p>0.10$, $R^2=0.19$, see Figure 6) and no relationship between deer density and diversity (N=12, $p>0.10$, $R^2=0.00$, see Figure 7). Again, we had too few data points to conduct an ANOVA on the effects of urbanization on small mammal diversity though the data suggest that no relationship appears to exist (see Figure 8).

Figure 6 Patch size and small mammal community diversity at forest sites.

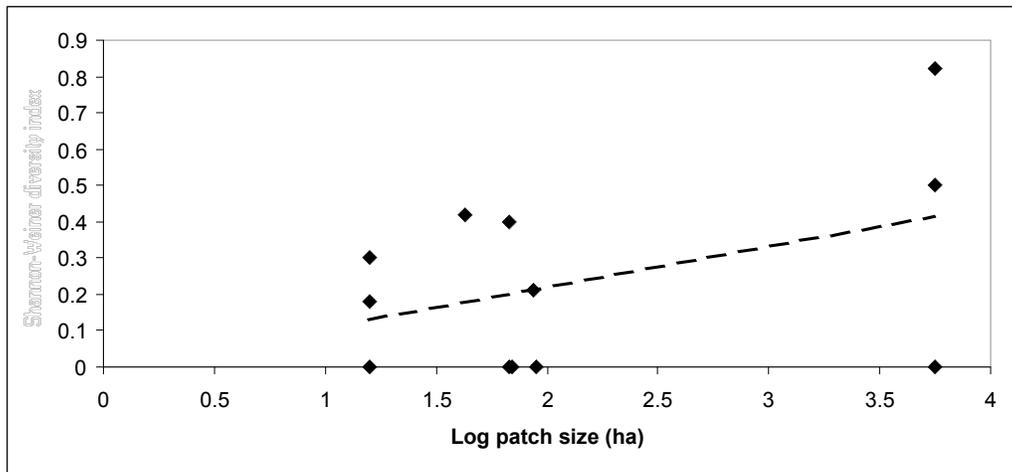


Figure 7 Deer density and small mammal community diversity at forest sites.

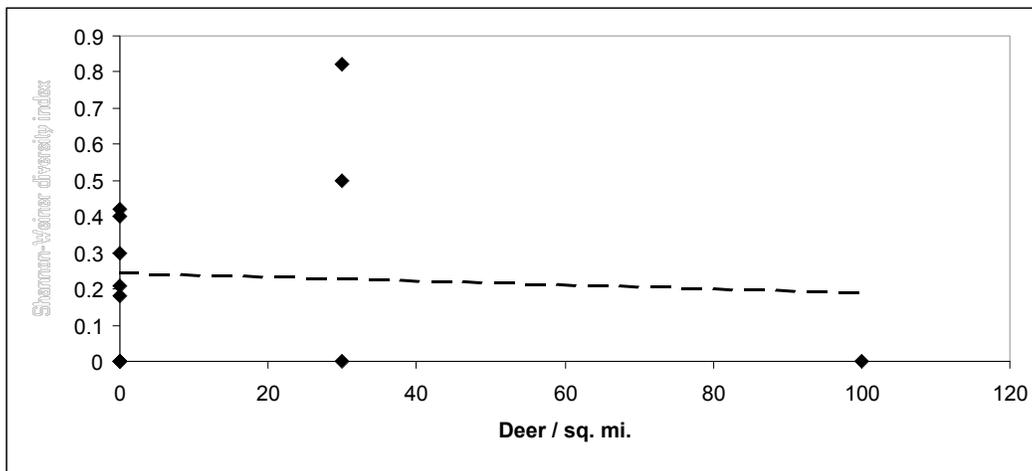
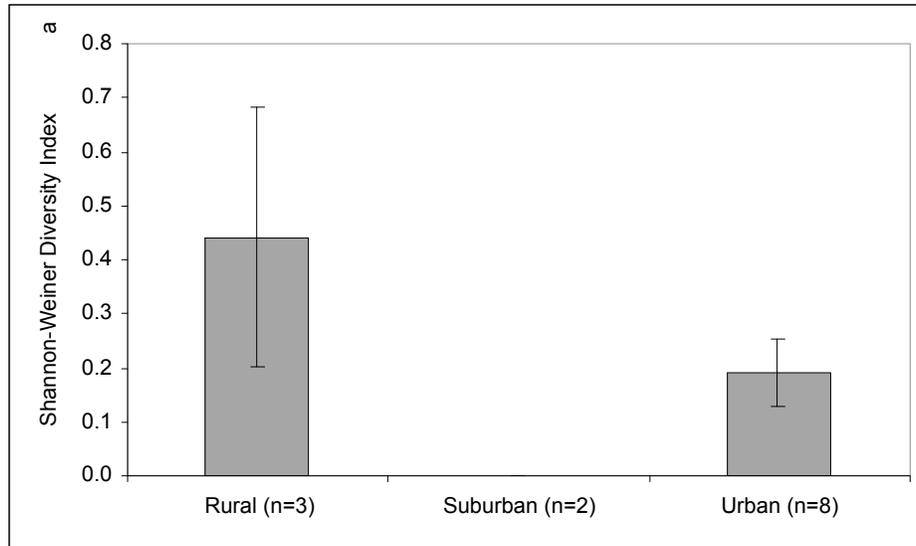


Figure 8 Urbanization and small mammal community diversity at forest sites.



Microhabitat correlates of *P. leucopus* density in a grassland-shrubland mosaic site

The Fort Tilden grassland survey was located on a mosaic of beach grass, shrubs, and scrub vegetation that offered an opportunity to evaluate capture rates in different habitat types. Of 144 trap nights, 45 took place in beach grass, 54 in shrubs (vegetation <5ft tall, ground cover >50% woody vegetation), and 45 in scrub (vegetation >5ft tall, ground cover >25% trees). White-footed mice were found at significantly higher densities in shrub and scrub vegetation than in beach grass (2x3 Chi square test, N=55 captures, p<0.05).

Botfly parasitism

Botflies (likely *Cuterebra* spp., Diptera: Cuterebridae) were very prevalent among small mammals, particularly *P. leucopus*, at the New York Botanical Garden, with 60 percent of captured animals harboring botflies in September of 2005. These parasites were far less prevalent at other sites, and only one other site had more than 5 percent of animals visibly infected (Spring Creek High Marsh, with 18 percent). With only two surveys having large numbers of botflies and one of them – Spring Creek High Marsh – consisting of only one night of trapping, it is impossible to discern any clear patterns from our data.

Discussion

Effects of habitat type on small mammal diversity and density

Results from our study indicate that habitat type has a strong influence on small mammal community diversity across the New York Metropolitan Region, even at vastly different spatial scales. On a regional scale, small mammal communities in salt marsh, forest, and shrubland macrohabitats shared clear similarities within themselves and distinct differences from each other, with salt marshes containing the highest diversity of any habitat type. All survey sites of the same habitat type contained similar species, and all of the species we trapped – with the exception of *P. leucopus* – were present in only a subset of the habitat types. For instance, we trapped *B. brevicauda* only in forests, *R. norvegicus* only in salt marshes, and *M. pennsylvanicus*

in all habitat types except forests. Habitat type also had a clear influence on small mammal communities on a microhabitat scale. Shrubland and salt marsh habitats consistently contained distinct small mammal communities, even when they were separated by only a few meters. This finding is consistent with previous studies suggesting that microhabitat structure is a major determinant of which small mammal species are present at a particular site (Dueser and Shurgart 1978; Kaufman *et al.* 1983; Bowers and Dooley 1996; Kantak 1996; Payne and Caire 1999; Anderson *et al.* 2003).

Habitat type did not have nearly the same influence on overall small mammal density, as we did not find any significant differences in density between the four habitat types. On a microhabitat scale, however, differences in small mammal density were significant in at least one location. At Fort Tilden, small patches of shrubs showed statistically significant differences in *P. leucopus* density from the surrounding beach grass matrix. Similar differences in microhabitats may have existed at other sites, though we did not note them at the time. As a caveat, we should note that Fort Tilden may not be representative of other locations, because during 294 trap-nights we trapped only one species of small mammal (*P. leucopus*). These data, together with the absences of certain species from entire habitat types, lend support to the hypothesis that habitat type influences the density of individual species. That small mammal density remained regionally consistent despite these individual species variations implies that as one species declines in abundance from one habitat to the next, one or several others replace it at roughly similar densities.

Effects of microhabitat on small mammal density and diversity

Such habitat selection by small mammal species is a well-documented phenomenon that may explain the coexistence of multiple small mammal species across macrohabitats (Rosenzweig 1973; M'Closkey 1976). Previous research has implicated predation risk (Thompson 1982*a, b*; Kotler 1984*a*; Price 1984; Brown *et al.* 1988; Hughes *et al.* 1994), physiological constraints (Yunger *et al.* 2002), interspecific competition (Kotler 1984*b*; Bowers *et al.* 1987; Younger *et al.* 2002; Stapp 1997) and temporal partitioning (Brown *et al.* 1989; Brown *et al.* 1994) as underlying mechanisms for the macro- and microhabitat selection of individual small mammal species. There is a considerable literature suggesting that predation risk may be the most influential dynamic structuring small mammal communities (Kotler 1984*a, b*; Brown *et al.* 1988, Kotler *et al.* 1991, Morris and Davidson 2000, Roche 1999). For example, some rodent species may avoid foraging in unsheltered habitat, like meadows or forest edges, where they are more likely to be detected by avian and other vertebrate predators (Kotler *et al.* 1991; Vasquez 1994; Thorson *et al.* 1998; Morris and Davidson 2000; Orrock *et al.* 2000). Other species may hold behavioral or morphological adaptations allowing them to forage in open areas for longer periods of time (Thompson 1982*a*). While data from our study do not implicate any one of these mechanisms in particular, the observed differences in distribution among the surveyed habitat types and microhabitats invite future research to test these different hypotheses.

Our results suggest that the microhabitat feature most influential to *P. leucopus* densities, and perhaps to other small mammal species densities, is the structure and density of the understory cover. Previous studies on *P. leucopus* microhabitat affinities have reached similar conclusions (Dueser and Shurgart 1978; Kaufman *et al.*, 1983; Merriam and Lanoue 1990; Anderson *et al.* 2003; Arthur *et al.* 2003). Kaufman *et al.* (1983) found that *P. leucopus* individuals were captured more frequently near trees with large shrubs, trees with small shrubs, large shrubs alone, and at the bases of rocks, logs, stumps, and fallen trees; they also avoided

areas with grass. These findings suggest that *P. leucopus* strongly selects for microhabitats with a complex vertical structure, and subsequent studies have refined this hypothesis to state that *P. leucopus* select for dense understory cover (Kaufman *et al.* 1983; Barnum *et al.* 1992; Flowerdew and Ellwood 2001; Brannon 2005). In our study, sites with denser understory cover tended to have higher *P. leucopus* densities. For example, the New York Botanical Garden forest had a much thicker understory and a much higher *P. leucopus* density than either Black Rock Forest or the Marshlands Conservancy forest. Similarly, the Marshlands Conservancy meadow, with its tall (3-5 ft) and profuse herbaceous growth, had a much higher density of *P. leucopus* than the adjoining Marshlands Conservancy forest. Sites with extremely low *P. leucopus* densities – outside of regularly-flooded salt marshes – also shared the common feature of sparse understory cover. At the time of our survey, grasses at Floyd Bennett Field (where we captured no animals in 294 trap-nights) were only about 6 inches tall, and the forest at Marshlands Conservancy (where we captured one animal in 147 trap-nights) was notably lacking in understory cover.

While Floyd Bennett Field's lack of cover was striking, it should be noted that there are several other factors that could potentially explain the absence of small mammals from the site. Small mammals may not be able to cross the asphalt runways to colonize the site's grasslands, since previous studies have indicated that roads may serve as dispersal barriers for many small mammals (Oxley *et al.* 1974; Merriam *et al.* 1989). Other studies have shown that mowed grass can also act as a dispersal barrier for some small mammals, suggesting that the grasslands at Floyd Bennett Field may simply not be suitable habitat for many small mammal species (Krohne and Hoch 1999; Mahan and O'Connell 2005). The site's artificial lighting may also have reduced small mammal densities, as increased nocturnal illumination (from both natural and artificial sources) can reduce small mammal activity (Vasquez 1994). It is more difficult to find alternate explanations for the extremely low density of small mammals in Marshlands Conservancy's forest. Small mammals were found at high densities in the adjacent meadow where urbanization, patch size, and other factors were identical, and small mammals utilized similar forests at high densities elsewhere in the region. The only obvious feature unique to the forest is the lack of understory cover, which is probably a direct result of Marshland Conservancy's extremely high deer density (100 deer/mile²).

The effects of deer density on forest communities of small mammals

In our study, deer density had a significant negative correlation with small mammal density in forests, and there is some reason to believe that this relationship was causally related. Studies from a variety of different habitats have indicated an inverse relationship between ungulate and small mammal densities. Flowerdew and Ellwood (2001) found that increased densities of deer in wooded areas of England decreased small mammal densities. The authors suggested two potential pathways for ungulates to reduce small mammal densities: by the modification or removal of habitat (which can remove nesting materials, shelter from predators, and alter the balance of competition between species), and/or through competition for food resources (Flowerdew and Ellwood 2001). Browsing activity of Reeves' muntjac (*Muntiacus reevesi*), roe deer (*Capreolus capreolus*), and fallow deer (*Dama dama*) caused reductions in the canopy cover, mid-cover, and ground cover of the study site, resulting in a significant decline in native bank vole populations (Flowerdew and Ellwood 2001). Keesing (1998), working in a savannah in Kenya, found that small mammal populations inside ungulate exclosures increased

significantly over a 2-year period. Keesing concluded that, because of the similarities in diets of small mammal and ungulate species, removing ungulates caused an increase in the quantity or quality of food available to small mammals (Keesing 1998). In rangelands in the northern United States, ungulate grazing and vegetation trampling have been reported to decrease vegetation cover for small mammals (Grant *et al.* 1982). Similarly, Rooney and Waller (2003) found that white-tailed deer (*Odocoileus virginianus*) acted as a keystone herbivore in various ecological communities, with their increased presence leading to profound habitat alterations. *O. virginianus* browsing has been reported to reduce overall vegetative cover, particularly of shrubs and saplings, and to decrease the diversity of the understory herb community – effectively reducing the habitat’s vertical complexity (Rooney and Waller 2003; Giuliano and Homyack 2004). Given this typical removal of understory cover by deer at high densities and the preference of *P. leucopus* for habitats with high levels of vertical complexity (Kaufman *et al.* 1983; Barnum *et al.* 1992; Flowerdew and Ellwood 2001; Brannon 2005); the tendency of some small mammal species to avoid unsheltered habitat due to predation risk (Kotler *et al.* 1991; Vasquez 1994; Thorson *et al.* 1998; Morris and Davidson 2000; Orrock *et al.* 2000); and the confirmed presence of small mammal predators in several sites (Brady 1994; Gompper *et al.* 2003; A. Beall, personal communication), it is plausible that increased *O. virginianus* density is causally linked to the reduced small mammal densities in forests we observed in the New York Metropolitan region.

Our data are not conclusive, however, as the apparent relationship between deer density and small mammals may be driven by a third factor such as predator densities. Notably, coyotes were present in all sites where deer density was high and small mammal density low, and they were absent from all sites where small mammal populations were high. Since we do not have data on coyote or other predator densities at different sites, we cannot at this stage evaluate their influence on small mammal communities.

Small mammal communities in salt marshes

This study was the first to evaluate how effective restoration efforts at Big Egg Marsh have been at re-establishing a small mammal community representative of those found in other salt marshes in the region. Overall, the restoration appears to have been successful, as *P. leucopus* and *R. norvegicus* utilized the site and both were found at other salt marshes in the region. *M. pennsylvanicus* was either absent from Big Egg or present at a sufficiently low density to avoid capture in 147 trap-nights. Since few *M. pennsylvanicus* were captured in Spring Creek and none at the Marshlands Conservancy salt marsh, the apparent absence of the species in the restored marsh may simply reflect the low capture probability for a species at low densities – not the absolute absence of the species (there were no significant differences in *M. pennsylvanicus* capture rates between the Big Egg, Spring Creek, and Marshlands Conservancy salt marshes: 2x3 Chi Square; $p > 0.10$). *R. norvegicus*, being a non-native invasive, may not be a desirable species from a conservation point of view, but the species was commonly found in salt marshes in the region. That rats were present at the Big Egg marsh restoration area therefore makes the restoration a success in the sense that the area is fairly representative of other marshes in the region.

Interestingly, all four *R. norvegicus* captured at the Big Egg marsh restoration site were juveniles, while we captured only adult *R. norvegicus* in other salt marshes. The recent restoration activities at Big Egg Marsh created new salt marsh habitat in areas that were previously underwater (Frame and Adamo 2004). While we did not observe any overt

differences in vegetative cover between Big Egg and other salt marsh study sites, it is possible that the restored area is not yet equal in vegetative or soil quality to other marshes. In many small mammals, individuals dispersing outside established habitat, or into poorer quality habitat, are typically younger or lighter in weight than resident individuals (Gaines and McClenaghan 1980). That we captured only juvenile rats at Big Egg suggests that the restoration area may not yet be able to support as diverse and numerous a small mammal community as other salt marshes in the region; that we captured any animals, however, indicates that the site is capable of supporting, at least temporarily, some small mammal populations.

Several studies have enumerated the small mammal species associated with salt marshes, and these have mostly considered the animals present in frequently flooded areas to be transients, not residents (Johnston 1956; Fislser 1960; Shure 1970; Takekawa 2003). The daily flooding in low marshes is typically considered a major limiting factor for residence, and previous studies have noted that small mammal food sources and breeding activities tend to be restricted in low marshes (Dueser *et al.* 1978). Other studies, however, have indicated that rats and meadow voles inhabit low marsh areas on a long-term basis (Shure 1971; Howell *et al.* 1984).

Our data provide partial support for the hypothesis that small mammals are permanent residents of some salt marshes. We captured *M. pennsylvanicus* at significantly higher densities in the Sandy Hook low marsh than in the adjacent upland vegetation, where we captured none (Fisher's exact test, $p < 0.05$). As traps in the upland vegetation remained open from evening high tide through the morning, we had ample opportunity to trap animals moving into the low marsh at low tide and retreating to upland vegetation during high tide. That we did not suggest that *M. pennsylvanicus* are permanent residents of the Sandy Hook low salt marsh, and not just transient visitors nesting above the tide line at least in autumn. Data from other sites are less clear. At Marshlands Conservancy *M. pennsylvanicus* was found in *Phragmites* reeds bordering the low marsh but not in the low marsh itself, and at Spring Creek we captured *M. pennsylvanicus* in both the low marsh and the adjacent *Phragmites*. At no point did we capture the same individual in both habitats. Our data also suggest that rats may have been permanent residents of low marshes. We captured *R. norvegicus* at significantly higher densities in all low marshes than in adjacent upland sites, where we captured none. These data suggest that individuals of the species do not leave low marshes – at least not in favor of upland vegetation. Data from *P. leucopus* in salt marshes suggest that at least some animals of this species are transients, as we captured one individual in both Sandy Hook low marsh and in the adjacent shrubland. Although we could not determine the frequency of such movement events, our data suggest that these events are fairly rare since we only captured an individual in adjacent low marsh/upland sites once in 997 trap-nights. Overall these results do not conclusively determine that small mammals are permanent residents in salt marshes, but they suggest that *M. pennsylvanicus* and *R. norvegicus* can be.

The effects of urbanization and patch size on forest communities of small mammals

Remarkably, our data suggest that urbanization and patch size have no direct influence on small mammal diversity. These findings are decidedly contrary to the recognized consequences of habitat fragmentation, which typically include an overall reduction in species diversity (Saunders *et al.* 1991; Iida and Nakashizuka 1995; Laurance *et al.* 2002; Fahrig 2003). One possible explanation for the persistence of small mammals is that competitors and predators are more likely to be lost through the fragmentation process (Nupp and Swihart 1996; Rosenblatt *et al.* 1999). Many urbanized patches may also contain sufficiently large and heterogeneous habitats to support a diverse small mammal community (Johnson *et al.* 1979; Clark *et al.* 1998).

Furthermore, the survival of *P. leucopus* populations in fragmented landscapes may be due to an apparent flexibility in territorial behavior: in habitat patches with very high densities, home ranges decrease in size and have a much higher amount of overlap (Nadeau 1981; Wolff 1985). Adler and Wilson (1987) also suggested that *P. leucopus* exhibit a flexible demographic structure that may enable them to survive in poor quality habitat. If other small mammal species exhibit similar traits (and *M. pennsylvanicus* do; Ostfeld and Canham 1995), then small mammals may be more resilient to urbanization and fragmentation than other taxa.

As with deer density and understory cover, patch size had a significant influence on overall small mammal density. Urbanization often fragments habitat and decreases patch sizes, and with more data we may expect to find significantly higher densities in urban patches than in more rural, likely larger, patches. Such findings are mostly in accordance with previous studies on small mammal responses to urbanization, which have found increased densities in smaller and more isolated patches (Foster and Gaines 1991; Yahner 1992; Nupp and Swihart 1996; Bowers and Matter 1997; Nupp and Swihart 1998, 2000; Mossman and Waser 2001). *P. leucopus* in forest patches exhibit an inverse correlation with patch size, with a peak density occurring in patches less than 2 ha (Nupp and Swihart 1996). In addition, Barko *et al.* (2003) found higher small mammal capture rates in sites surrounded by a higher percentage of urban habitat, with most captures occurring in small patches directly adjacent to urban development. Higher small mammal densities in urban areas may be caused by the presence of barriers like roads, sidewalks, and landscaping. In a constricted urban landscape, small mammals may have minimal opportunities for emigration, creating patches with high abundances (Adler and Levins 1994; Barko *et al.* 2003).

Elevated small mammal densities have been thought to indicate high quality habitat (Ostfeld *et al.* 1985; Krohne and Hoch 1999; Carey and Harrington 2001), and they may also support higher densities of predators (such as raptors, snakes, and mammalian carnivores) that are often targeted in conservation efforts. In our study, small mammal densities in some small urban forest patches were as much as 19 times higher than those in large, intact, rural forests. Such high densities in more restricted urban sites can potentially lead to a variety of non-desirable effects. High small mammal densities may reduce (or even prevent) regeneration of mast seeding tree species (Ostfeld *et al.* 1996), and they can also lead to detrimental crowding effects or reduction in genetic variation (Krebs 1973; Gaines *et al.* 1997; Krohne and Hoch 1999; Mossman and Waser 2001; Barko *et al.* 2003). Without a more comprehensive understanding of urban ecosystems, it is unclear whether the high densities of small mammals we observed in small, urban natural areas lead to conservation benefits or unfavorable ecological effects.

Conclusion

Our results largely concur with recent studies emphasizing the ecological value of urban natural areas, but drawing any definite conclusions from our data about the effects of urbanization and patch size on small mammal communities is not yet fully warranted. First of all, these effects are limited to forests, as we did not have sufficient data to perform similar analyses in other habitats. Second, and perhaps more importantly, our survey methods may not have been conducive to determining true species richness. Our traps were baited specifically for species that feed on seeds and nuts, and our captures therefore likely under-represented insectivores and other species not attracted to seeds and nuts. This problem might have been exacerbated by the number of trap-nights that we used to complete a survey (147 trap-nights), which may not have been sufficient to fully sample insectivorous species at low densities. Such species may in fact be

negatively influenced by urbanization and reduced patch size, but these effects would not have been detectable in our data. Since species that live at low density are often of greater conservation concern than more commonly found species, these shortcomings are not insubstantial. This point is especially important because management strategies for a natural area are often based on the species of conservation concern found within its boundaries; missing some species therefore means management efforts may not be optimized for an area. As we did not find higher abundances of low density or rare small mammal species in rural study sites than in urban and suburban sites, our results suggest that natural areas across all levels of urbanization have similar conservation value. This is surely not the case. Though we did not capture rare species during our surveys in rural areas, island biogeography and conservation theory suggest that such species are almost certainly more prevalent in large, rural forests as opposed to fragmented, urban forests. Nonetheless, our results are compelling because they indicate that small, urban forests can support mostly intact small mammal communities. Non-native small mammal species, such as *R. norvegicus* or the house mouse *Mus musculus*, were no more prevalent in urban forests (with low levels of garbage) than they were in more intact forests. Some rare species may be missing, and generalist species may be found at atypically high densities, but species that are most common in more intact natural areas are most common in small urban patches.

Future Research

There are several factors that may have had a substantial influence on small mammal communities in urban habitat patches, though we were not able to completely explore them within the time constraints of the study. One theme we frequently encountered in our surveys was the invasion of urban and suburban habitats by non-native species. In forest habitat, invasive earthworms may alter the structure of leaf litter in ways that are particularly detrimental to small mammals (A. Beall, personal communication). Although we did not have the data to fully evaluate this hypothesis, the Marshlands Conservancy forest plot possessed a high density of earthworms (A. Beall, personal communication) and an almost total absence of small mammals, while meadow vegetation at the same location supported a high density of small mammals. While these observations suggest that the influence of invasive earthworms is limited to forest communities of small mammals, they imply a potential impact that invites future study.

Non-native plant species and small mammal predators are likely to exercise substantial influence on small mammal communities across a wide range of habitat types, and these effects are likely to vary along an urban-to-rural gradient. The replacement of native plant species with non-native invasive species in urban green spaces may alter or even eliminate microhabitat features important to one or more small mammal species, modifying the site's small mammal community. Small mammal predators affect small mammal communities both by direct predation and by altering competitive dynamics by selectively preying on certain species. Data on predator densities may therefore help explain small mammal community dynamics at many sites in the New York Metropolitan region, especially with coyote populations expanding in the northeast (Gompper 2002). We plan to explore the effects of both predator densities and vegetation on small mammal communities more fully in the future, for example through camera trapping and vegetation transects.

Quantifying vegetation will also be vital in confirming the negative relationships between *O. virginianus* density, understory cover, and small mammal density we observed in the study.

Furthermore, we had relatively few data points from sites where *O. virginianus* were present and aim to survey more sites with higher deer densities than found in New York City urban areas.

As we mentioned in the Discussion, our current trapping protocol may be better suited for gathering population abundance data on seed-eating small mammals than for surveying all small mammal species in a community. One of the ways we could improve future data collection on insectivorous species is by using additional trapping methods (Block *et al.* 1998). Since Sherman and other live traps baited with seeds and nuts may systematically over-represent seed- and nut-eating species, and under-represent shrews and other insectivores, pitfall traps may offer a good complement as they tend to over-represent shrews and other more active species. Pitfall traps used in conjunction with Sherman traps could gather a more complete picture of small mammal communities, and they could verify and improve species richness data without losing the ability to analyze population data in detail when combined with seed-baited Sherman traps (Anthony *et al.* 2005).

Finally, even though alterations to our trapping methods and collection of other data (i.e., vegetation) should add precision to the data we collect, the best way to improve our results is simply to increase the number of sites surveyed. In the 2006 field season, we plan to conduct surveys in additional parks within New York City, sample more rural areas, and resample sites that we surveyed this year. Since New York City does not support sizable deer or carnivore populations, we also plan to survey urban sites in Philadelphia where deer and predators are present. We hope to increase the number of sample sites in salt marshes, shrublands, and grasslands; additional data from these habitats will allow similar analyses as we conducted on forest small mammal communities, thereby substantially strengthening the value of our data. Though these surveys will require considerable effort, we will be working throughout the summer and plan to expand our research program in the coming field season.

References

- Adler, G. H., and R. Levins. 1994. "The island syndrome in rodent populations." *Quarterly Review of Biology*. 69: 473 – 490.
- Adler, G.H. and M.L. Wilson. 1987. "Demography of a Habitat Generalist, the White-Footed Mouse, in a Heterogeneous Environment." *Ecology*. 68(6): 1785 – 1796.
- Allan, B.F., Keesing, F., and R.S. Ostfield. 2003. "Effect of Forest Fragmentation on Lyme Disease Risk." *Conservation Biology*. 17 (1): 267–272.
- American Society of Mammalogists Animal Care and Use Committee (ACUC). 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. *Journal of Mammalogy* 79(4): 1416-1431.
- Anderson, C.S., Cady, A.B., and D.B. Meikle. 2003. "Effects of vegetation structure and edge habitat on the density and distribution of white-footed mice (*Peromyscus leucopus*) in small and large forest patches." *Canadian Journal of Zoology*. 81(5): 897 – 904.
- Anthony, N.M., Ribic, C.A., Bantz, R., and T. Garland, Jr. 2005. "Comparative effectiveness of Longworth and Sherman live traps." *Wildlife Society Bulletin*. 33(3): 1 – 9.
- Arthur, A.D., Pech, R.P., Drew, A., Gifford, E., Henry, S., and A. McKeown. 2003. "The effect of increased ground-level habitat complexity on mouse population dynamics." *Wildlife Research*. 30(6): 565 – 572.
- Barko, V.A., Feldhamer, G.A., Nicholson, M.C., and D.D. Kevin. 2003. "Urban Habitat: a determinant of white-footed mouse (*Peromyscus leucopus*) abundance in southern Illinois." *Southeastern Naturalist*. 2(3): 369 – 376.
- Barnum, S.A., Manville, C.J., Tester, J.R., and W.J. Carmen. 1992. "Path Selection by *Peromyscus leucopus* in the presence and absence of vegetative cover." *Journal of Mammalogy*. 73(4): 797 – 801.
- Bellows, A. S., Pagels, J. F., J. C. Mitchell. 2001. "Macrohabitat and microhabitat affinities of small mammals in a fragmented landscape on the upper coastal plain of Virginia." *American Midland Naturalist*. 146: 345 – 360.
- Bender, D. J., T. A. Contreras, and L. Fahrig. 1998. "Habitat loss and population decline: a meta-analysis of the patch size effect." *Ecology*. 79: 517 – 533.
- Bengston, D., Fletcher, J., and Nelson, K. 2004. "Public policies for managing urban growth and protecting open space: policy instruments and lessons learned in the United States." *Landscape and Urban Planning*. 69: 271 – 286.
- Block, W.M., Morrison, M.L., and P.E. Scott. 1998. "Development and Evaluation of Habitat Models for Herpetofauna and Small Mammals." *Forest Science*. 44(3): 430 – 437.
- Bowers, M.A. and J.L. Dooley. 1999. "A controlled hierarchical study of habitat fragmentation: responses at the individual, patch, and landscape scale." *Landscape Ecology*. 14: 381 – 389.
- Bowers, M.A. and S.F. Matter. 1997. "Landscape ecology of mammals: relationships between density and patch size." *Journal of Mammalogy*. 78: 999 – 1013.
- Bowers, M.A., Thompson, D.B., and J.H. Brown. 1987. "Spatial organization of a desert rodent community: food addition and species removal." *Oecologia*. 72 (1): 77 – 82.
- Brady, J.F. 1994. *Black Rock Forest deer population management report (1984-1994)*. Unpublished report, Black Rock Forest. Cornwall, N.Y.
- Brannon, M.P. 2005. "Distribution and Microhabitat of the Woodland Jumping Mouse, *Napaeozapus insignis*, and the White-footed Mouse, *Peromyscus leucopus*, in the Southern Appalachians." *Southeastern Naturalist*. 4(3): 479 – 486.

- Brown, J.S., Kotler, B.P., Smith, R.J., and W.O. Wirtz II. 1988. "The effects of owl predation on the foraging behavior of heteromyid rodents." *Oecologia*. 76(3): 1432 – 1939.
- Brown, J. S. 1989. "Desert rodent community structure: a test of four mechanisms of coexistence." *Ecological Monographs*. 59: 1 – 20.
- Brown, J.S., Kotler, B.P., and W.A. Mitchell. 1994. "Foraging theory, patch use, and the structure of a Negev Desert granivore community." *Ecology*. 75(8): 2286 – 2300.
- Burke, M., Berkley, B., Crane, T., Goldfarb, L., and Alvarez, M. 2004. "Spring Creek ecosystem restoration: the reclamation of an urban salt marsh." Poster presentation at the 89th conference of the Ecological Society of America, August 1-6 2004, Portland, OR. <http://abstracts.co.allenpress.com/pweb/esa2004/document/?ID=39867>. Last accessed 12/9/2005.
- Burns, C.E. 2005. "Behavioral ecology of disturbed landscapes: The response of territorial animals to relocation." *Behavioral Ecology*. 16(5): 898-905.
- Burns, C. E., B. J. Goodwin, and R. S. Ostfeld. 2005. "A prescription for longer life? Bot fly parasitism of the white-footed mouse." *Ecology*. 86: 753 – 761.
- Burt, W.H., and Grossenheider, R.P. 1976. *Peterson Field Guides Mammals*. Houghton Mifflin Company: New York, NY.
- Butts, S. R., and W. C. McComb. 2000. "Associations of forest-floor vertebrates with coarse woody debris in managed forests of western Oregon." *Journal of Wildlife Management*. 64: 94 – 105.
- Carey, A. and C. Harrington. 2001. "Small mammals in young forests: implications for management for sustainability." *Forest Ecology Management*. 154: 289 – 309.
- Carey, A. B., and M. L. Johnson. 1995. "Small mammals in managed naturally young, and old-growth forests." *Ecological Applications*. 5: 336 – 352.
- Clark, B.K., Clark, B.S., Homerding, T.R., and W.E. Munsterman. 1998. "Communities of small mammals in six grass-dominated habitats of Southeastern Oklahoma." *American Midland Naturalist*. 139 (2): 262 – 268.
- Childs, J.E., T.G. Ksiazek, C.F. Spiropoulou, J.W. Krebs, S. Morzunov, G.O. Maupi, K.L. Gage, P.E. Rollin, J. Sarisky, R.E. Enscore, J.K. Frey, C.J. Peters, and S.T. Nichol. 1994. "Serologic and genetic identification of *Peromyscus maniculatus* as the primary reservoir for a new hantavirus in the southwestern United States." *Journal of Infectious Diseases*. 169: 2171 – 2180.
- Cook, R.P. 1989. *Mammals of Gateway National Recreation Area*. USDI, National Park Service, Gateway National Recreation Area. 8 pp booklet.
- Cousins, S. 1982. Species size distributions of birds and snails in an urban area. Pp. 99 – 109 in: R. Bornkamm, J. Lee, and M. Seward (eds), *Urban Ecology*. Oxford: Blackwell Scientific Publications.
- Dickman, C.R., and C.P. Doncaster. 1987. "The Ecology of Small Mammals in Urban Habitats. I. Populations in a Patchy Environment." *Journal of Animal Ecology*. 56(2): 629 – 640.
- Donahue, J.G., J. Piesman, and A. Spielman. 1987. Reservoir competence of white-footed mice for Lyme disease spirochetes. *American Journal of Tropical Medicine and Hygiene*. 36: 92 – 96.
- Dueser, R.D. and H.H. Shugart Jr. 1978. "Microhabitats in a forest-floor small mammal fauna." *Ecology*. 59(1): 89 – 98.

- Dueser, R.D., Porter, J.H., and T.F. Wieboldt. 1978. "Species-Habitat Associations and Succession Vectors for Small Mammal and Land Bird Populations on Assateague Island National seashore." National Park Service Technical Report. 60 pp.
- Eccard, J. and H. Ylönen. 2003. "Interspecific competition in small rodents: from populations to individuals." *Evolutionary Ecology*. 17: 423 – 440.
- Elbin, S.B., and Koontz, F.W. 1998. "Status of grassland birds breeding on restored grasslands at Floyd Bennett Field, Gateway National Recreation Area." Final Report. Wildlife Conservation Society. 67pp.
- Gaines, M.S., and McClenaghan, L.R. 1980. "Dispersal in small mammals." *Annual Review of Ecology and Systematics*. 11: 163 – 196.
- Gaines, M.S., Diffendorfer, J.E., R.D., Tamarin, R.H., and T.S. Whittam. 1997. "The effects of habitat fragmentation on the genetic structure of small mammal population." *Journal of Heredity*. 88(4): 294 – 304.
- Getz, L.L. 1961. "Factors Influencing the Local Distribution of Shrews." *American Midland Naturalist*. 65(1): 67 – 88.
- Giuliano, W.M., and J.D. Homyack. 2004. "Short-term grazing exclusion effects on riparian small mammal communities." *Rangeland Ecology and Management*. 57(4): 346 – 350.
- Goldstein-Golding, E. 1991. "The ecology and structure of urban greenspaces." Pp. 392-411 in: S. Bell and H. Mushinsky (eds), *Habitat Structure*. London: Chapman and Hall.
- Gompper, M.E. 2002. *The Ecology of Northeast Coyotes: Current Knowledge and Priorities for Future Research*. WCS Working Paper No. 17, Bronx, NY. <http://www.wcs.org/science>
- Gompper, M.E., Goodman, R.M., Kays, R.W., Ray, J.C., Fiorello, C.V., and S.E. Wade. 2003. "A Survey of the Parasites of Coyotes (*Canis latrans*) in New York based on Fecal Analysis." *Journal of Wildlife Diseases*. 39(3): 712 – 717.
- Google. 2005. Google Maps. <http://www.maps.google.com>. Last accessed 12/15/2005.
- Grant, W.E., Birney, E.C., French, N.R., and D.M. Swift. 1982. "Structure and productivity of grassland small mammal communities related to grazing-induced changes in vegetative cover." *Journal of Mammalogy*. 63: 248 – 260.
- Fahrig, L. 2003. "Effects of Habitat Fragmentation on Biodiversity." *Annual Review of Ecology, Evolution and Systematics*. 34: 487 – 515.
- Fisler, G.F. 1960. "Changes in Food Habits of Short-eared Owls Feeding in a Salt Marsh." *Condor*. 62 (6): 486 – 487.
- Flowerdew, J.R. and S.A. Ellwood. 2001. "Impacts of woodland deer on small mammal ecology." *Forestry*. 74(3): 277 – 287.
- Foster, J. and M.S. Gaines. 1991. "The effects of a successional habitat mosaic on a small mammal community." *Ecology*. 72(4): 1358-1373.
- Frame, G.W., and Adamo, D. 2004. "A participatory approach to salt-marsh restoration in Jamaica Bay, New York." Chapter 4, p.7, in Selleck, J. (ed) *Natural Resource Year in Review – 2004*. National Park Service. <http://www2.nature.nps.gov/YearinReview/index.html>.
- Francel, K., Castelberry, S., and Ford, W. 2004. "Small mammal communities of high elevation central Appalachian wetlands." *American Midland Naturalist* 151: 388-398.
- Gaines, M.S., and L.R. McClenaghan, Jr. 1980. "Dispersal in Small Mammals." *Annual Review of Ecology and Systematics*. 11: 163 – 196.
- Hollander, J. and Vander Wall S. 2004. "Effectiveness of six species of rodents as dispersers of single leaf pinon pine (*Pinus monophylla*)." *Oecologia* 138: 57-65.

- Howell, P.T. 1984. "Use of Salt Marshes by Meadow Voles." *Estuaries*. 7(2): 165 – 170.
- Hughes, J. J., Ward, D., and M. R. Perrin. 1994. "Predation risk and competition affect habitat selection and activity of Namib Desert gerbils." *Ecology*. 75 (5): 1397 – 1405.
- Iida, S. and Nakashizuka, T. 1995. " Forest fragmentation and its effect on species diversity in sub-urban coppice forests in Japan ." *Forest Ecology and Management*. 73(1-3): 197-210.
- Johnson, W.C., Schreiber, R.K., and R.L. Burgess. 1979. "Diversity of small mammals in a powerline right-of-way and adjacent forest in East Tennessee." *American Midland Naturalist*. 101 (1): 231 – 235.
- Johnston, R.F. 1956. "Predation by short-eared owls on a salicornia salt marsh." *Wilson Bulletin*. 68: 91 – 102.
- Kamler, J.F., and D.S. Pennock. 2004. "Microhabitat selection of *Peromyscus leucopus* and *P. maniculatus* in mid-successional vegetation." *Transactions of the Kansas Academy of Science*. 107(1): 89 – 92.
- Kantak, G. E. 1996. "Microhabitats of two *Peromyscus* (deer and white-footed mice) species in old fields and prairies of Wisconsin." *Canadian Field Naturalist*. 110: 322 – 325.
- Kaufman, D.W., Peterson, S.K., Fristik, R., and G.A. Kaufman. 1983. "Effect of Microhabitat Features on Habitat Use by *Peromyscus leucopus*." *The American Midland Naturalist*. 110(1): 177 – 185.
- Keeling, M.J., and Gilligan, C.A. 2000. "Metapopulation dynamics of bubonic plague." *Nature*. 407: 903 – 906.
- Keesing, F. 2008. "Impacts of ungulates on the demography and diversity of small mammals in central Kenya." *Oecologia*. 116: 381 – 389.
- Kitchings, J.T., and D.J. Levy. 1981. "Habitat patterns in a small mammal community." *Journal of Mammalogy*. 62(4): 814 – 820.
- Klee, R. V., Mahoney, A. C., Christopher, C. C., and G. W. Barrett. 2004. "Riverine Peninsulas: An Experimental Approach to Homing in White-footed Mice (*Peromyscus leucopus*)." *The American Midland Naturalist* 151(2): 408–413.
- Kotler, B. P. 1984a. "Harvesting rates and predatory risk in desert rodents: a comparison of two communities on different continents." *Journal of Mammalogy*. 65(1): 91 – 96.
- Kotler, B. P. 1984b. "Risk of predation and the structure of desert rodent communities." *Ecology*. 65(3): 689 – 701.
- Kotler, B. P., Brown, J.S., and O. Hasson. 1991. "Factors affecting gerbil foraging behavior and rates of owl predation." *Ecology*. 72: 2249 – 2260.
- Krebs, C.J., Gaines, M.S., Keller, B.L., Meyers, J.H., and R. H. Tamarin. 1973. "Population cycles in small rodents." *Science*. 179, 35 – 41.
- Krohne, D.T., Dubbs, B.A., and Baccus, R. 1984. "An analysis of dispersal in an unmanipulated population of *Peromyscus leucopus*." *American Midland Naturalist*. 112: 146–158.
- Krohne, D. T., and G. A. Hoch. 1999. "Demography of *Peromyscus leucopus* populations on habitat patches: the role of dispersal." *Canadian Journal of Zoology*. 77:1247–1253.
- Kunick, W. 1982. "Comparison of the flora of some cities of central European lowlands." Pp. 255-275 in: R. Bornkamm, J. Lee and M. Seward (eds), *Urban Ecology*. Oxford: Blackwell Scientific Publications.
- Laurance W.F., Lovejoy T.E., Vasconcelos H.L., Bruna E.M., Didham R.K., Stouffer P.C., Gascon C., Bierregaard R.O., Laurance S.G., and Sampaio E. 2002. "Ecosystem decay of Amazonian forest fragments: a 22-year investigation." *Conservation Biology*. 16(3): 605-618.

- McCloskey, R.T. 1976. "Community Structure in Sympatric Rodents." *Ecology*. 57(4): 728 – 739.
- McCarley, W. H. 1954. "The Ecological Distribution of the *Peromyscus leucopus* Species Group in Eastern Texas." *Ecology*. 35(3): 375 – 379.
- McDonnell, M.J., Rudnicki, J.L., and Koch, J.M. 1990. *Permanent Forest Reference Plot System: Pelham Bay Park and Van Cortlandt Park, Bronx, New York. Volume 3, Vegetation Analysis and Description*. Report to New York City Department of Parks and Recreation. 50pp.
- McDonnell, M.J., Pickett, S.T.A., Groffman, P., Bohlen, P., Pouyat, R.V., Zipperer, W.C., Parmelee, R.W., Carreiro, M.M., and Medley, K. 1997. "Ecosystem processes along an urban-to-rural gradient." *Urban Ecosystems*. 1:21-36.
- Mahan, C.G., and T.J. O'Connell. 2005. "Small Mammal Use of Suburban and Urban Parks in Central Pennsylvania." *Northeastern Naturalist*. 12(3): 307 – 314.
- Manning, J. A., and W. D. Edge. 2004. "Small mammal survival and downed wood at multiple scales in managed forests." *Journal of Mammalogy*. 85:857 – 859.
- Marks, M., Lapin, B., and J. Randall. 1994. "*Phragmites australis* (*P. communis*): threats, management and monitoring." *Natural Areas Journal*. 14: 285 – 294.
- Marzluff, J. M., R. Bowman, and R. Donnelly. 2001. A historical perspective on urban bird research: trends, terms, and approaches. Pp.1 – 18 in: J. M. Marzluff, R. Bowman, and R. Donnelly, editors. *Avian ecology in an urbanizing world*. Kluwer Academic: Norwell, Massachusetts, USA.
- Merriam, G., Kozakiewicz, M., Tsuchiya, E., and K. Hawley. 1989. "Barriers as boundaries for metapopulations and demes of *Peromyscus leucopus* in farm landscapes." *Landscape Ecology*. 2(4): 227 – 235.
- Merriam, G. and A. Lanoue. 1990. "Corridor use by small mammals: field measurement for three experimental types of *Peromyscus leucopus*." *Landscape Ecology*. 4(2-3): 123 – 131.
- Mills, J.N. and J. E. Childs. 1998. "Ecologic Studies of Rodent Reservoirs: Their Relevance for Human Health." *Emerging Infectious Diseases*. 4(4): 529 – 553.
- Morin, P. 1999. *Community Ecology*. Malden, MA: Blackwell Science Publications, 424pp.
- Morris, D. W., and D. L. Davidson. 2000. "Optimally foraging mice match patch use with habitat differences in fitness." *Ecology*. 81(1): 2061 – 2066.
- Mossman, C.A. and P.M. Waser. 2001. "Effects of habitat fragmentation on population genetic structure in the white-footed mouse (*Peromyscus leucopus*)." *Canadian Journal of Zoology*. 79: 285 – 295.
- Nadeau, J., R. Lombardi, and R. H. Tamarin. 1981. "Population structure and dispersal of *Peromyscus leucopus* on Muskeget Island." *Canadian Journal of Zoology*. 59:793-799.
- New York City Parks Department. 2001. "Hunter Island, Pelham Bay Park." http://nycgovparks.org/sub_your_park/historical_signs/hs_historical_sign.php?id=11859. Last accessed 12/10/2005.
- Nupp, T. E., and R. K. Swihart. 1996. "Effect of forest patch area on population attributes of white-footed mice (*Peromyscus leucopus*) in fragmented landscapes." *Canadian Journal of Zoology*. 74:467-472.
- Nupp, T.E., and R.K. Swihart. 1998. "Effects of forest fragmentation on population attributes of white-footed mice and eastern chipmunks." *Journal of Mammalogy*. 79: 1234 – 1243.
- Nupp, T.E., and R.K. Swihart. 2000. "Landscape-level correlates of small-mammal assemblages in forest fragments of farmland." *Journal of Mammalogy*. 81: 512 – 526.

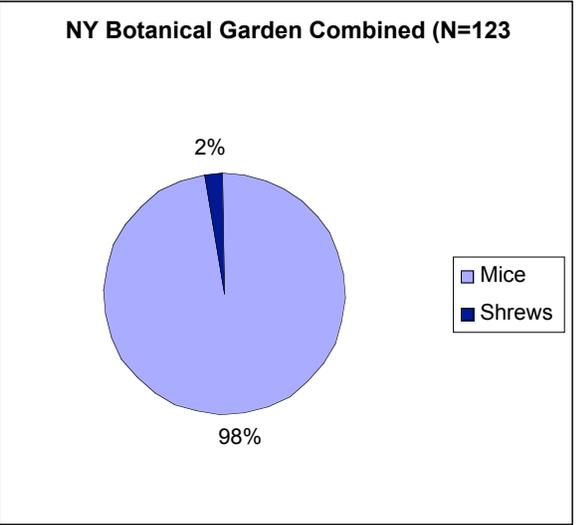
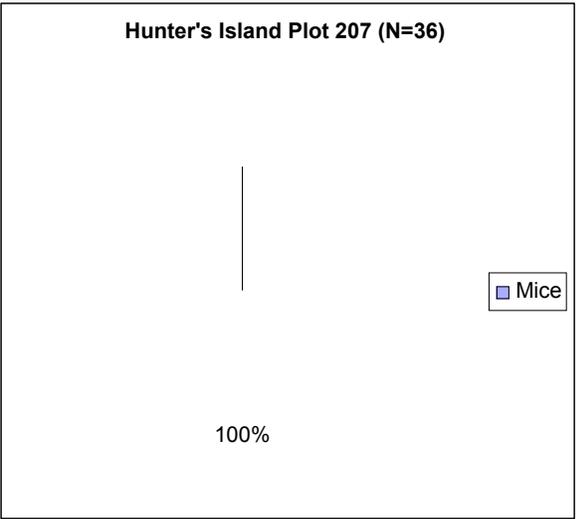
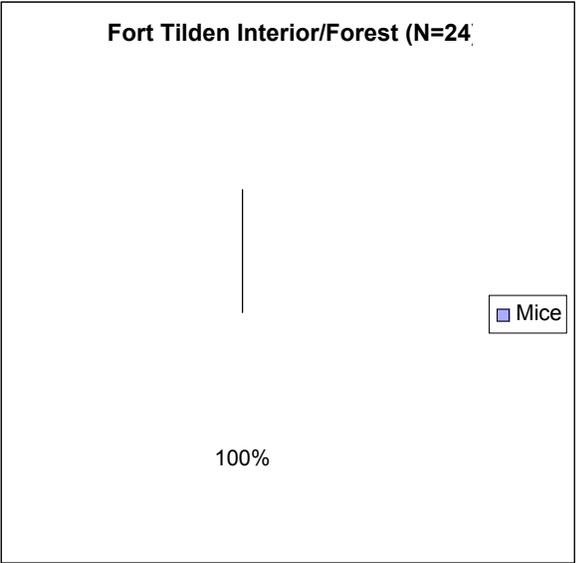
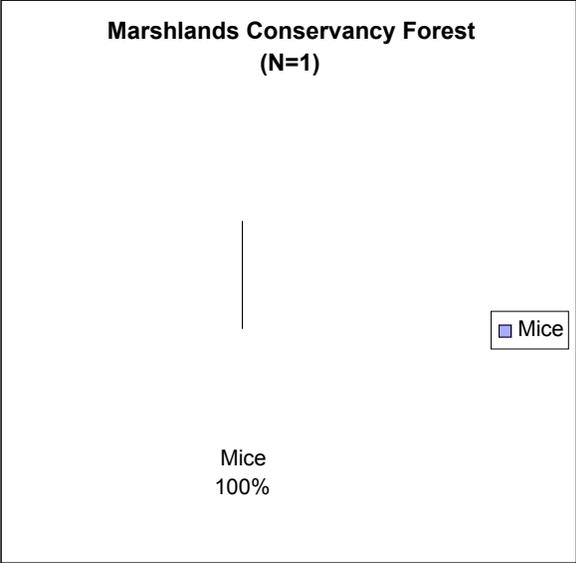
- Obara, H., Hirata, H., and M. Okuzaki. 1977. "An aspect of the existence of mammals in urban ecosystems." Pp. 173 – 187. *In* M. Numata (ed.). Tokyo project: Interdisciplinary studies of Urban Ecosystems in the Metropolis of Tokyo. Tokyo.
- Orrock, J. L., J. F. Pagels, W. J. McShea, and E. K. Harper. 2000. "Predicting presence and abundance of a small mammal species: the effect of scale and resolution." *Ecological Applications*. 10: 1356- 1366.
- Ostfeld, R.S., W.Z. Lidicker, and E.J. Heske. 1985. "The relationship between habitat heterogeneity, space use, and demography in a population of California voles." *Oikos*. 45: 433 – 442.
- Ostfeld, R.S., and C.D. Canham. 1995. "Density-dependent processes in meadow voles: an environmental approach." *Ecology*. 76(2): 521 – 532.
- Ostfeld, R. S., Jones, C. G. and J.O. Wolff. 1996. "Of mice and mast: ecological connections in eastern deciduous forests." *BioScience*. 46: 323-330.
- Ostfeld, R. S., and F. Keesing. 2000. "Biodiversity and disease risk: the case of Lyme disease." *Conservation Biology*. 14: 722 – 728.
- Otis, D.L., Burnham, K.P., White, G.C., and D.R. Anderson. 1978. "Statistical Inference from Capture Data on Closed Animal Populations." *Wildlife Monographs*. 62: 1 – 135.
- Oxley, D.J., Fenton, M.B. and Carmody, G.R. 1974. The effects of roads on populations of small mammals. *J. Appl. Ecol.* 11: 51-59.
- Payne, T., and W. Caire. 1999. "Species Diversity of Small Mammals in the Tallgrass Prairie Preserve, Osage County, Oklahoma." *Proceedings of the Oklahoma Academy of Sciences*. 79:51-59.
- Pearce, J. and Venier, L. 2005. "Small mammals as bioindicators of sustainable boreal forest management." *Forest Ecology and Management*. 208: 153 – 175.
- Pickett, S.T.A., Cadenasso, M.L, Grove, J.M., Nilon, C.H., Pouyat, R.V., Zipperer, W.C., and R. Costanza. 2001. "Urban ecological systems: linking terrestrial ecological, physical, and socioeconomic components of metropolitan areas." *Annual Review of Ecological Systematics*. 32: 127-157.
- Price, M. V. 1984. "Microhabitat use in rodent communities: predator avoidance or foraging economics?" *Netherlands Journal of Zoology*. 34(1): 63 – 80.
- Pusenius, J., Ostfeld, R. and Keesing, F. 2000. "Patch selection and tree-seedling predation by resident versus immigrant meadow voles." *Ecology*. 8: 2951 – 2956.
- Rexstad, E. A., and K. P. Burnham. 1991. User's guide for interactive program CAPTURE. Colorado Cooperative Wildlife Research Unit, Colorado State University, Fort Collins, CO. 29 pp.
- Rich, S.M., Kilpatrick, C.W., Shippee, J.L., and Crowell, K.L. 1996. "Morphological differentiation and identification of *Peromyscus leucopus* and *P. maniculatus* in Northeastern North America." *Journal of Mammalogy*. 77(4): 985-991.
- Roche, B. E. 1999. "Route choice by deer mice (*Peromyscus maniculatus*): Reducing the risk of auditory detection by predators." *American Midland Naturalist*: 142: 194 – 197.
- Roman, C.T., Niering, W.A., and R.S. Warren. 1984. "Salt marsh vegetation change in response to tidal restriction." *Environmental Management*. 8:141-150.
- Rooney, T.P., and D.M. Waller. 2003. "Direct and indirect effects of white-tailed deer in forest ecosystems." *Forest Ecology and Management*. 181: 165 – 173.

- Rosenblatt, D. L., E. J. Heske, S. L. Nelson, D. M. Barber, M. A. Miller, and B. MacAllister. 1999. "Forest fragments in east-central Illinois: islands or habitat patches for mammals?" *American Midland Naturalist*. 141:115–123.
- Rosenzweig, M. L. 1973. "Habitat selection experiments with a pair of coexisting heteromyid species." *Ecology*. 54:111 – 117.
- Saunders, D.A., Hobbs, R.J., and Margules, C.R. 1991. "Biological consequences of ecosystem fragmentation: A review." *Conservation Biology*. 5(1): 18-32.
- Sauvajot, R., Buechner, M., Kamradt, D., and Schonewald, C. 1998. "Patterns of human disturbance and response by small mammals and birds in chaparral near urban development." *Urban Ecosystems*. 2: 279 – 297.
- Shanholtzer, G.F. 1974. "Relationships of vertebrates to salt marsh plants." pp. 463 – 474. In R.J. Reimold and W.H. Queen (eds.). *Ecology of Halophytes*. Academic Press, New York.
- Schnabel, Z.E. 1938. The estimation of the total fish population of a lake; *American Mathematics Monthly*. 45: 348 – 352.
- Schnurr, J.L., Canham, C.D., Ostfeld, R.S., and R.S. Inouye. 2004. "Neighborhood analyses of small mammal abundance and activity: impacts on tree seed predation and seedling establishment." *Ecology*. 85(3): 741 – 755.
- Shure, D.J. 1970. "Ecological Relationships of Small Mammals in a New Jersey Barrier Beach Habitat." *Journal of Mammalogy* 51(2): 267 – 278.
- Shure, D.J. 1971. "Tidal Flooding Dynamics: Its influence on Small Mammals in Barrier Beach Marshes." *American Midland Naturalist*. 85(1): 36 – 44.
- Stapp, P. 1997. "Community Structure of Shortgrass-Prairie Rodents: Competition risk or intraguild predation?" *Ecology*. 78(5): 1519 – 1530.
- StatsDirect Ltd. 2005. StatsDirect statistical software. <http://www.statsdirect.com>. England: StatsDirect Ltd.
- Tessier, N., Noël, S., and Lapointe, F.J. 2004. "A new method to discriminate the deer mouse (*Peromyscus maniculatus*) from the white-footed mouse (*Peromyscus leucopus*) using species-specific primers in multiplex PCR." *Canadian Journal of Zoology*. 82(11): 1832-1835.
- Thompson, S. D. 1982a. "Microhabitat utilization and foraging behavior of bipedal and quadrupedal heteromyid rodents." *Ecology*. 63: 1303 – 1312.
- Thompson, S. D. 1982b. "Structure and species composition of desert heteromyid rodent species assemblages: effects of a simple habitat manipulation." *Ecology*. 63:1313 – 1321.
- Thorson, J.M., Morgan, R.A., Brown, J.S., and J.E. Norman. 1998. "Direct and indirect cues of predatory risk and patch use by fox squirrels and 13-lined ground squirrels." *Behavioral ecology*. 9(2): 151 – 157.
- Takekawa, J. Y., M. A. Bias, I. Woo, S. A. Demers, and E. E. Boydston. 2003. Small mammal survey at Big Lagoon, Muir Beach, Marin County, CA. Unpubl. Progr. Rep., U. S. Geological Survey, Vallejo, CA. 25pp.
- Vasquez, R.A. 1994. "Assessment of predation risk via illumination level – facultative central place foraging in the cricetid rodent *Phyllotis darwini*." *Behavioral Ecology and Sociobiology*. 34: 375 – 381.
- Whitaker, J.O., Jr. 1996. *National Audubon Society Field Guide to North American Mammals*. Chanticleer Press Inc.: New York, NY.

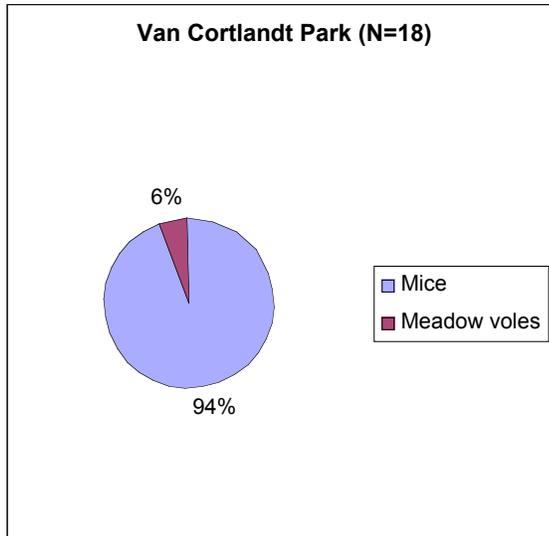
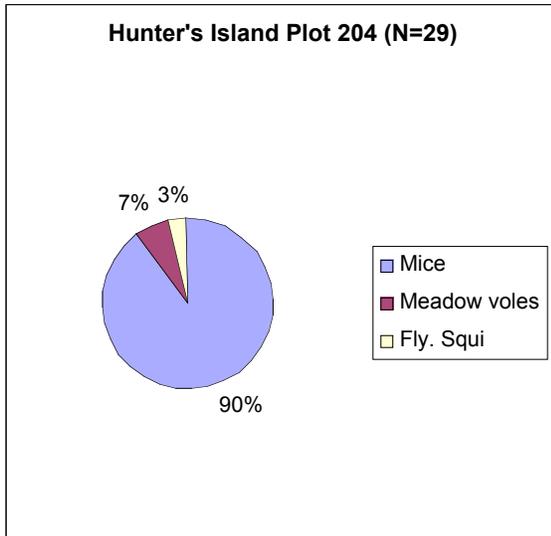
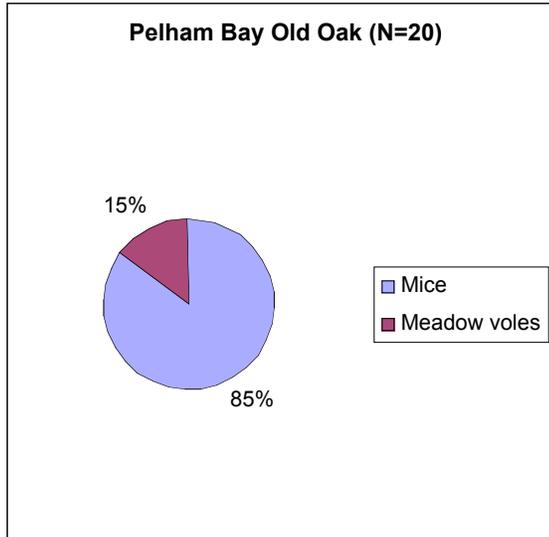
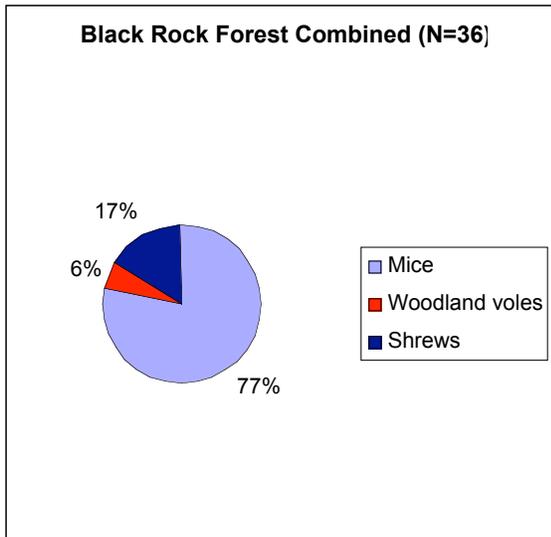
- White, G.C., Anderson, D.R., Burnham, K.P., and D.L. Otis. 1982. "Capture-recapture and removal methods for sampling closed populations." Los Alamos National Laboratory, Los Alamos, New Mexico.
- Wolff, J.O. 1985. "The effects of density, food, and interspecific interference on home range size in *Peromyscus leucopus* and *Peromyscus maniculatus*." *Canadian Journal of Zoology*. 63(11): 2657 – 2662.
- Yahner, R.H. 1992. Dynamics of a small mammal community in a fragmented forest." *American Midland Naturalist*. 127: 381 – 391.
- Yunger, J.A., Meserve, P.L., and J. R. Gutierrez. 2002. "Small-mammal foraging behavior: mechanisms for existence and implication for population dynamics." *Ecological Monographs*. 72(4): 561 – 577.

Appendix I: Species composition for each study site

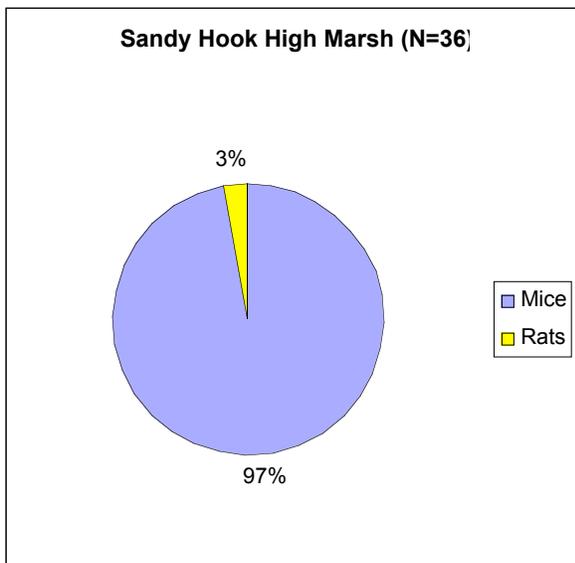
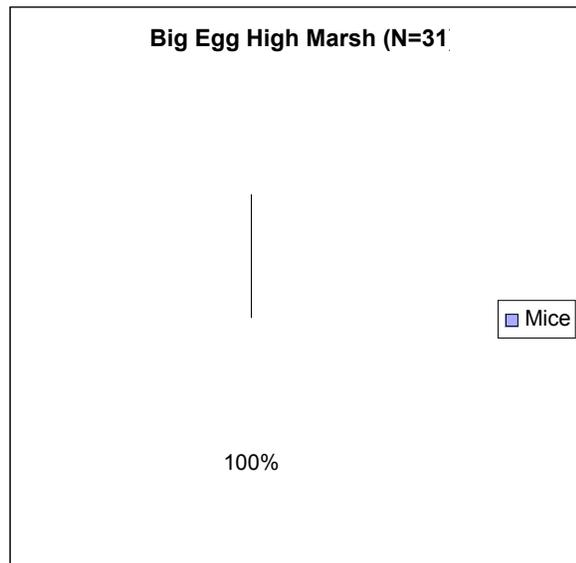
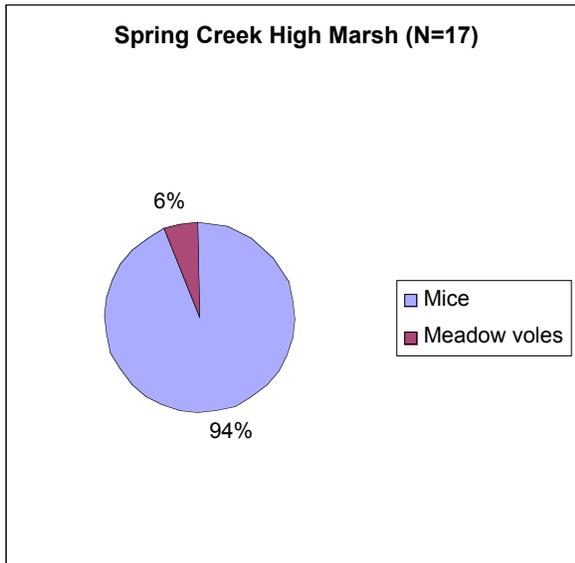
Forests



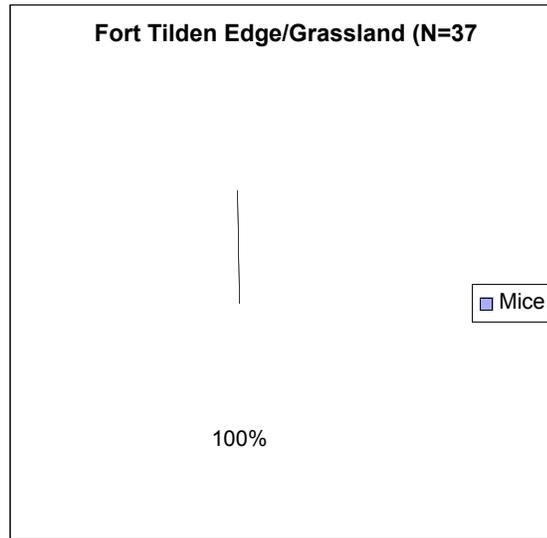
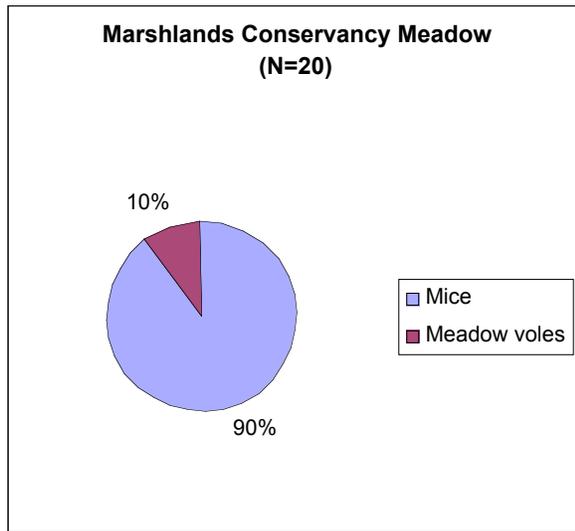
Forests (continued)



Shrubland

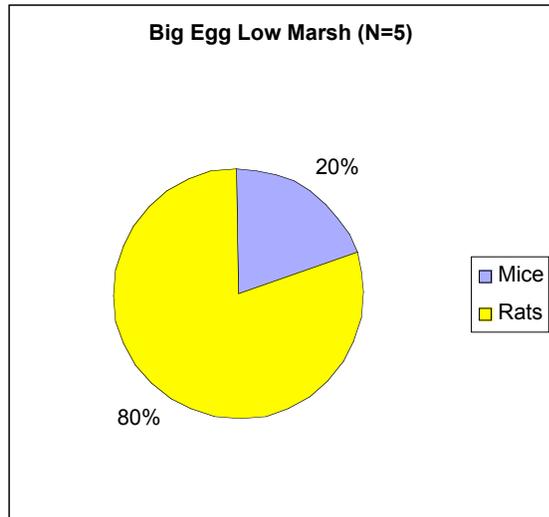
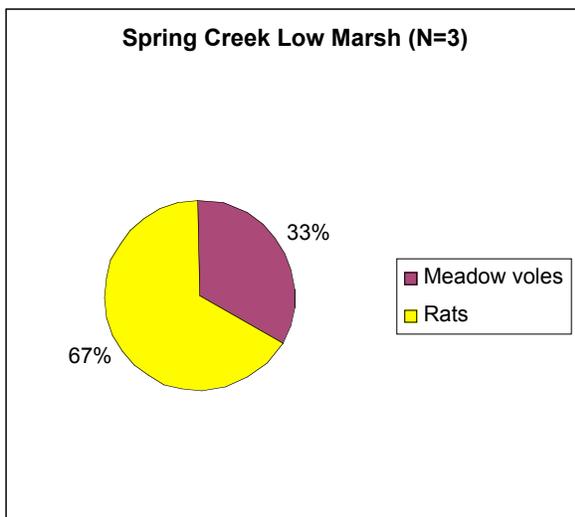
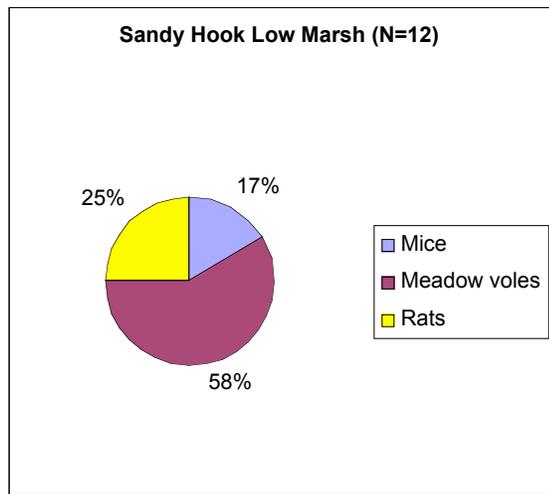
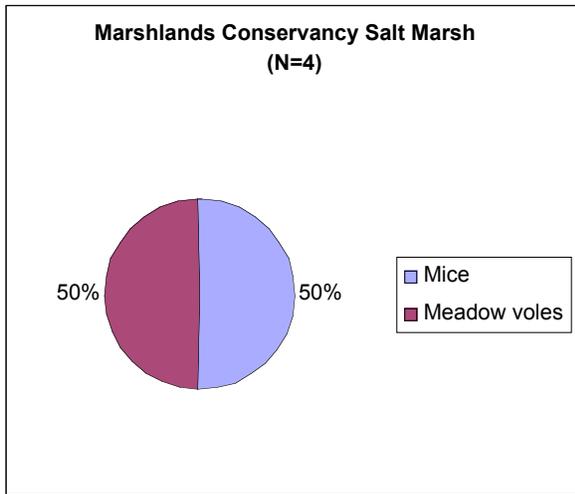


Grassland

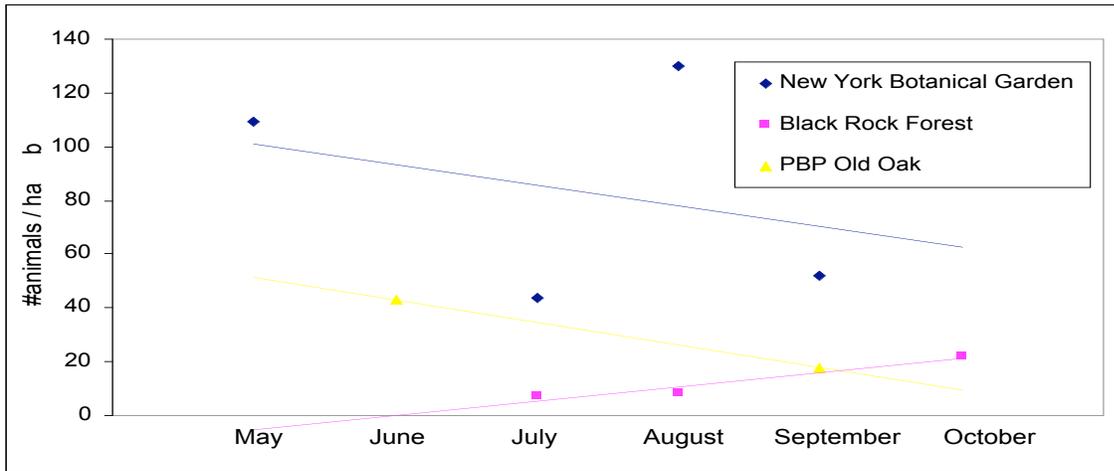


N.B.: Floyd Bennett Field is not listed as no animals were caught there.

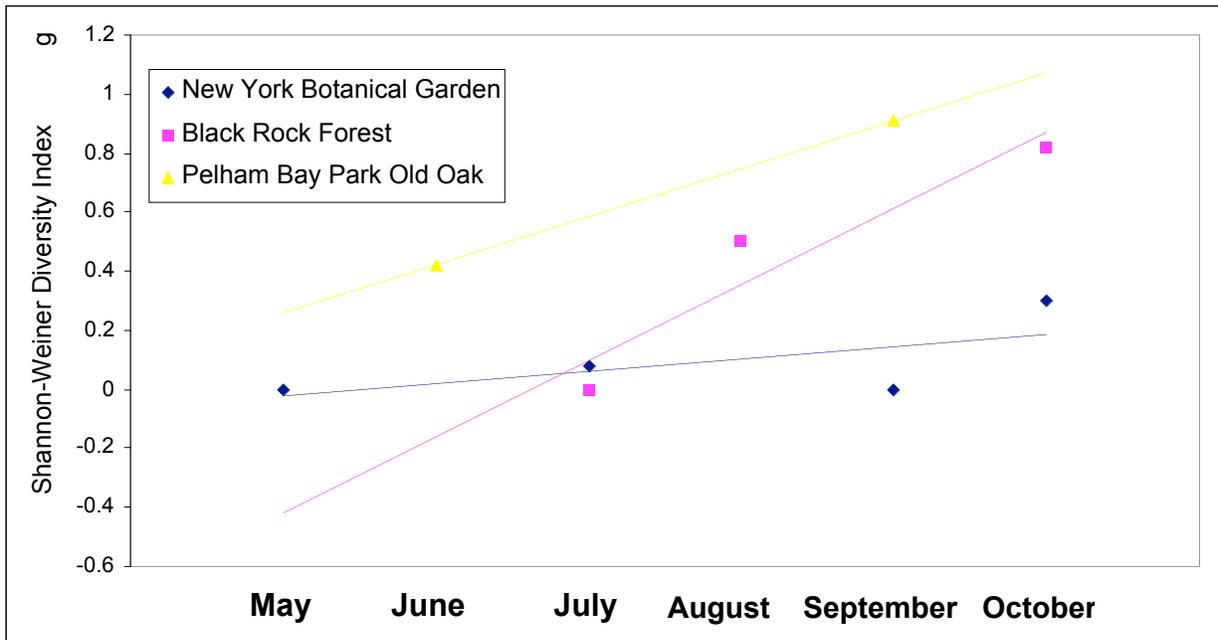
Salt Marsh



Appendix II: Effects of seasonality on small mammal communities



Effects of seasonality on small mammal density (2004 – 2005) from all sites sampled in different seasons.



Effects of seasonality on small mammal diversity (2004 – 2005) from all sites sampled in different seasons.

Appendix III: Urban classification definitions from Marzluff *et al.* (2001)

Table 1.1. Standardized terms that describe major points along the gradient of urbanization. These terms are most meaningful at relatively large ($>1\text{km}^2$), landscape scales. Other attributes of each class and suggestions for subdividing classes are provided in the text. Residential human density refers to the density of humans occupying living quarters (dwellings) in the area.

Term	Percent built	Building density	Residential human density
Wildland	0-2	0	$<1 / \text{ha}$
Rural / exurban	5-20	$<2.5 / \text{ha}$	$1-10 / \text{ha}$
Suburban	30-50	$2.5-10 / \text{ha}$	$>10 / \text{ha}$
Urban	>50	$> 10 / \text{ha}$	$>10 / \text{ha}$