

Assessing small mammal abundance and diversity in North Dakota grasslands

by

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CHAPTER 1: GENERAL INTRODUCTION

INTRODUCTION

Throughout the prairies of North America, pristine grassland and wetland habitats have been reduced and fragmented by human practices, especially agriculture (Higgins 1977, Sugden and Beyersbergen 1984, Cowardin et al. 1985, Klett et al. 1988, Greenwood et al. 1995). These landscape changes have been linked to declines in many grassland- and wetland-associated passerine (Winter and Faaborg 1999, Herkert et al. 2003) and waterfowl (Greenwood et al. 1995, Beauchamp et al. 1996) species. Direct effects of habitat loss and fragmentation include reduced patch size, increased patch isolation, and increased habitat edge (Saunders et al. 1991, Faaborg et al. 1993) that affect settling patterns, density, and recruitment of these avian populations (Herkert 1994, Herkert et al. 2003). Habitat loss and fragmentation have resulted in increased nest predation as nesting birds and foraging predators are concentrated in remaining habitat patches (Cowardin et al. 1985, Sargeant and Raveling 1992, Greenwood et al. 1995, Beauchamp et al. 1996). Many researchers have hypothesized that small mammals, which also utilize grassland and wetland habitat patches, may serve as alternate prey for medium-sized predators and buffer predation on ground- and shrub-nesting birds and their eggs (Byers 1974, Weller 1979, Pehrsson 1986, Beintema and Muskens 1987, Marcstrom et al. 1988, Ackerman 2002). If this is the case, then increased avian nesting success and recruitment rates might be expected during periods of small mammal abundance (Byers 1974, Pehrsson 1986, Beintema and Muskens 1987, Summers and Underhill 1987, Crabtree and Wolfe 1988, Jarvinen 1990, Ackerman 2002). Alternatively, abundant small mammal populations might attract foraging predators or support greater local predator densities, thereby increasing predation pressure on nesting birds and their eggs (Roseberry and Klimstra 1970, Klimstra and Roseberry 1975, Greenwood et al. 1998, Wilson and Bromley 2001).

A major issue restricting our understanding of the role of small mammals in predator-prey interactions in prairie landscapes is a lack of tools to relate small-scale studies to large-scale landscape patterns. Traditional small mammal sampling methods, such as mark-recapture and removal surveys, are expensive and labor intensive, which limits the duration and the

spatial extent of small mammal studies. Track-based indices, which are correlated with small mammal abundance at the species level (Drennan et al. 1998, Glennon et al. 2002), may provide a useful alternative method of assessing relative abundance over large areas. Track-based indices are less expensive and labor intensive than mark-recapture or removal surveys, reduce disturbance of study organisms, and reduce exposure of researchers to animal-borne diseases (Drennan et al. 1998, Glennon et al. 2002). Further examination of the relationship between track-based indices and small mammal abundance is necessary to assess the utility of track-based indices.

Another approach to understanding the role of small mammals in predator-prey interactions is to better understand how small mammals utilize grassland habitat patches at multiple scales. At the macrohabitat level, for example, food availability, soil moisture, the amount of cover, and the dominant vegetation influence small mammal abundance, diversity, and distribution (Birney et al. 1976, Grant et al. 1977, Abramsky et al. 1979, Grant and Birney 1979). At the microhabitat level, small-scale patterns and heterogeneity in these characteristics play important roles in the abundance and distribution of different small mammal species within larger habitat patches (Getz 1961, Birney et al. 1976, Grant et al. 1977, Abramsky et al. 1979, Grant and Birney 1979, Kaufman et al. 1988, Snyder and Best 1988). Further quantification of small mammal habitat use at macrohabitat and microhabitat scales could be combined with recent research describing use of grassland patches by nesting waterfowl (Cowardin et al. 1985, Sargeant and Raveling 1992, Greenwood et al. 1995, Beauchamp et al. 1996) and foraging predators (Greenwood et al. 1999, Sovada et al. 1999, Sovada et al. 2000, Kuehl and Clark 2002, Phillips et al. 2003) to provide insight into the effects of spatial and temporal variability in small mammal abundance, diversity, and distribution on predator-prey interactions.

My research took place from May to August, 2001-2002, in the Missouri Coteau in western Stutsman County, North Dakota. Research was conducted on Waterfowl Production Areas (WPAs), which are managed to provide grassland and wetland habitats suitable for nesting waterfowl and other wildlife species of the Northern Great Plains. The native vegetation of the Missouri Coteau in central North Dakota is mixed-grass prairie (Euliss

1996). WPAs sometimes contain native prairie remnants, although most WPA lands are formerly cultivated and grazed areas that have been planted to native grasses, non-native cool-season grasses, or dense nesting cover (Duebbert and Lokemoen 1976). WPA management practices consist of burning, fertilization, grazing, scarification, or mowing, depending on land-use history and specific management goals (Euliss 1996).

The objectives of my research were: 1) to compare and evaluate three methods, mark-recapture, removal, and track tube surveys, of assessing small mammal abundance and diversity; 2) to develop regression models predicting small mammal abundance estimates as a function of track tube indices; 3) to investigate small mammal–habitat associations in upland and wet-meadow grassland habitats; and 4) to develop regression models predicting small mammal abundance and diversity as a function of macrohabitat- and microhabitat-level soil moisture and vegetation characteristics.

THESIS ORGANIZATION

This thesis consists of two manuscripts written with the intent of submission to the *Journal of Mammalogy*. Chapter 2 examines the relationship between track tube indices and abundance estimates generated from traditional mark-recapture and removal surveys. Chapter 3 examines small mammal abundance and diversity at macrohabitat and microhabitat levels in North Dakota grasslands. Each chapter was written by Andrew S. Wiewel and edited by Dr. W. R. Clark. Following the two manuscripts is Chapter 4, which provides general research conclusions and a discussion of small mammal prey biomass in grassland habitats. Literature cited in Chapters 1 and 4 is listed at the end of Chapter 4.

CHAPTER 2: ASSESSING SMALL MAMMAL ABUNDANCE USING POPULATION ESTIMATES AND TRACK TUBE INDICES

A paper to be submitted to the Journal of Mammalogy

Andrew S. Wiewel

ABSTRACT

In the Northern Great Plains small mammals are the primary prey of many medium-sized mammalian predators and potentially buffer predation on passerine and waterfowl species and their nests. By developing inexpensive and rapid sampling methods, we can better study small mammal populations at the large spatial and temporal scales necessary for understanding these complex predator-prey interactions. I compared a track tube survey method with traditional mark-recapture (live trapping) and removal (snap trapping) surveys and evaluated a track tube index, defined as the number of track tubes with identifiable small mammal tracks during a 4-night survey period, as a predictor of small mammal abundance estimates. Track tube surveys were less expensive than mark-recapture surveys (\$1.40/track tube, \$12.80/Sherman live trap), required less time ($\bar{X} = 438.4$ minutes/4-night survey, $SE = 34.32$) than mark-recapture ($\bar{X} = 687.8$ minutes/4-night survey, $SE = 54.95$) or removal ($\bar{X} = 636.7$ minutes/4-night survey, $SE = 21.78$) surveys, and reduced the exposure of technicians to animal-borne diseases by eliminating handling of small mammals. Meadow voles (*Microtus pennsylvanicus*) were the most commonly recorded species in each survey, but were underrepresented in track tube surveys (80.9% of mark-recapture captures, 76.7% of removal captures, 46.2% of track tube indices). In contrast, thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*) and Franklin's ground squirrels (*S. franklinii*) were overrepresented in track tube surveys (4.8% of mark-recapture captures, 8.5% of removal captures, 42.1% of track tube indices). Removal surveys captured more meadow voles ($\overline{M}_{t+1} = 84.82$, $SE = 9.87$) and more total small mammals ($\overline{M}_{t+1} = 110.53$, $SE = 10.04$) than mark-recapture surveys ($\overline{M}_{t+1} = 41.27$, $SE = 6.72$; $\overline{M}_{t+1} = 51.03$, $SE = 6.81$, respectively). However, population estimates generated from removal surveys of meadow voles ($\bar{N} = 124.9$, $SE = 13.3$) and of all small mammals ($\bar{N} = 164.8$, $SE = 13.2$) were not markedly different

than mark-recapture population estimates ($\bar{N} = 120.2$, SE = 12.8; $\bar{N} = 131.7$, SE = 13.0, respectively). Removal surveys also detected greater species richness ($\bar{S} = 5.00$, SE = 0.27) than mark-recapture ($\bar{S} = 3.97$, SE = 0.24) or track tube ($\bar{S} = 3.31$, SE = 0.21) surveys. Regression models revealed that the track tube index was a poor predictor of small mammal abundance estimates due to variation in the form (linear vs. curvilinear) and changes in the slope of the relationship between years. In addition, 95% prediction intervals indicated low precision when predicting abundance estimates from new track tube index observations. One possible improvement involves investigating the utility of track tube intrusions (the number of different individuals responsible for tracks in track tubes) as a predictor of small mammal abundance.

INTRODUCTION

In the Northern Great Plains small mammals are the primary prey of many medium-sized mammalian predators (Bekoff 1977, Larivière and Pasitschniak-Arts 1996, Greenwood et al. 1999, Sovada et al. 1999) and may buffer predation of passerine and waterfowl species and their nests (Byers 1974, Weller 1979, Pehrsson 1986, Beintema and Muskens 1987, Marcstrom et al. 1988, Ackerman 2002). Conversely, abundant small mammal populations may attract or sustain predator populations and lead to increased foraging pressure (Roseberry and Klimstra 1970, Klimstra and Roseberry 1975, Greenwood et al. 1998, Wilson and Bromley 2001). Consequently, estimating the abundance and diversity of small mammal populations is an integral step in understanding predator-prey interactions. Unfortunately, the cryptic and primarily nocturnal activity patterns of many small mammal species make abundance estimates expensive and difficult to obtain, especially at spatial and temporal scales suitable for studying predator-prey interactions. Thus, many researchers desire methods that reduce expense and effort while allowing the assessment of small mammal abundance and diversity across broad spatial and temporal scales.

Traditionally, small mammal populations have been sampled using mark-recapture or removal surveys, and estimates of abundance have been produced using models for closed or open populations (Jolly 1965, Seber 1965, Otis et al. 1978, Pollock et al. 1990). Mark-recapture and removal surveys are also commonly used to generate count-based indices of

abundance, such as the number of unique individuals captured (M_{t+1} , Otis et al. 1978), the total number of captures (n , Otis et al. 1978), or the minimum number known alive (MNKA, Krebs 1966). The use of count-based indices has been discouraged because of the negative bias of many indices (Nichols and Pollock 1983) and incomplete knowledge of the relationship between indices and true abundance (Nichols 1986, Anderson 2001). However, when data are sparse or capture probabilities are low, the known negative bias of count-based indices may be favored over the unreliability of estimator selection procedures and the unknown bias and low precision of abundance estimates generated under these conditions (Otis et al. 1978, Menkins and Anderson 1988, Pollock et al. 1990, Manning et al. 1995, Stanley and Burnham 1998, McKelvey and Pearson 2001). Count-based indices also have utility when researchers seek relative, rather than absolute, measures of abundance (Slade and Blair 2000). However, neither population estimates nor count-based indices produced from mark-recapture or removal surveys reduce the underlying expense and effort associated with sampling methods based on capturing animals.

Abundance indices may also be generated from indirect evidence of the presence of study organisms at a location, such as tracks. Track-based indices have been used to study the distribution (Justice 1961, Taylor and Raphael 1988, Boonstra et al. 1992, Sargeant et al. 1993, Sovada et al. 1995, Mabee 1998, Drennan et al. 1998, Engeman et al. 2000, Glennon et al. 2002, Kuehl and Clark 2002), behavior (Sheppe 1965, Kuehl and Clark 2002), and relative abundance (Lord et al. 1970, Quy et al. 1993, Sargeant et al. 1993, Drennan et al. 1998, Engeman et al. 2000, Glennon et al. 2002) of a variety of mammalian species. Track-based indices present researchers with several potential advantages when compared to population estimates or count-based indices, including reduced expense and labor, reduced sampling effort, reduced disturbance of study organisms, and reduced exposure of researchers to animal-borne diseases (Boonstra et al. 1992, Drennan et al. 1998, Glennon et al. 2002). However, the proposed utility of track-based indices is based on the assumption that the relationship between the index and true abundance is monotonic and relatively constant across space and time. If this assumption is true, and can be quantified, track-based indices may be a useful alternative to traditional small mammal survey methods. However, if this

assumption is false, the unknown bias of track-based indices would offset any potential benefits related to reduced expense and effort. Track-based indices may also have lower statistical power to detect changes in abundance than estimates generated from mark-recapture or removal surveys (Drennan et al. 1998), and there are no standard methods for determining the precision of track-based indices (Anderson 2001, but see Engeman et al. 1999). Examination of the advantages and disadvantages of track-based indices, including a rigorous investigation of the relationship between track-based indices and abundance estimates, is necessary to assess the utility of track-based indices. My research objectives were: 1) to investigate species-specific patterns in the number of individuals captured or detected, and the diversity of species captured or detected, by mark-recapture, removal, and track tube surveys; 2) to develop regression models predicting small mammal abundance estimates as a function of track tube indices; and 3) to investigate the relative efficiency of track tube surveys in comparison to mark-recapture and removal surveys.

STUDY AREA

Small mammal sampling was conducted on federally owned Waterfowl Production Areas (WPAs) in the Missouri Coteau physiographic region in western Stutsman County, North Dakota between May and August, 2001-2002. WPAs are managed to provide grassland and wetland habitats suitable for nesting passerine and waterfowl species and also provide habitat for numerous other wildlife species. The native vegetation of the Missouri Coteau in central North Dakota is mixed-grass prairie dominated by western wheatgrass (*Agropyron smithii*), needle and thread (*Hesperostipa comata*), big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), green needlegrass (*Nassella viridula*), prairie cordgrass (*Spartina pectinata*), and northern reedgrass (*Calamagrostis stricta*), and also containing a diverse mix of forbs such as Maximilian sunflower (*Helianthus maximiliani*) and Canada goldenrod (*Solidago canadensis*) (Euliss 1996). WPAs may contain native prairie remnants, although most WPAs are formerly cultivated and grazed areas that have been planted to native grasses, non-native cool-season grasses, or dense nesting cover (Duebbert and Lokemoen 1976). WPA management practices consist of burning, fertilization, grazing,

scarification, or mowing, depending on land-use history and management goals (Euliss 1996).

METHODS

Small mammal populations were studied on randomly selected WPAs in 2001 ($n = 5$) and 2002 ($n = 8$). To be considered for study, WPAs had to be ≥ 16 ha and contain at least one seasonal or semi-permanent wetland ≥ 3 ha. WPAs mowed or burned < 1 year prior to the beginning of each field season were not considered. Within each selected WPA, adjacent upland and wet-meadow habitats were identified using aerial photographs and ground-truthing. Paired upland and wet-meadow habitats, separated by ≥ 300 m to minimize the likelihood of small mammal dispersal between habitats, were selected for small mammal surveys. Selected WPAs were large (approximately 100–600 ha) and often contained multiple upland and wet-meadow habitat pairs suitable for this study. As a result, 2 pairs of upland and wet-meadow habitats were surveyed on 1 WPA in 2001 and 3 WPAs in 2002. High water levels during the 2001 field season limited the availability of suitable wet-meadow habitats on 3 WPAs; additional upland habitats were selected for sampling in these situations. In total, 8 upland and 4 wet-meadow habitats were surveyed in 2001, and 11 upland and 11 wet-meadow habitats were surveyed in 2002 (Appendix).

Mark-Recapture, Removal, and Track Tube Surveys

Small mammal surveys were conducted on each pair of upland and wet-meadow habitats over a two-week period. During the first week, mark-recapture surveys of small mammal populations were conducted using individual Sherman live traps (22.9 by 8.9 by 7.6 cm; H.B. Sherman Traps, Inc., Tallahassee, FL) placed at 10 m intervals in an 8 by 16 grid ($n = 128$ traps, grid = 1.05 ha). Rectangular trapping grids were chosen to best sample the relatively narrow wet-meadow habitat bordering wetlands. Closed traps were placed on each grid a minimum of 3 days prior to the beginning of sampling to allow small mammals to acclimatize to their presence. Each habitat was trapped for 4 consecutive nights, resulting in 512 trap nights/habitat/WPA. Traps were baited with a mixture of peanut butter, oats, and food-grade paraffin. Traps were checked before 10 AM each day, and captured animals were examined to determine species, age, reproductive condition, and weight. Captured animals

were uniquely marked in each ear with serially numbered metal ear tags (#1005-1; National Band and Tag Co., Newport, KY) or by toe clipping for species that could not be ear-tagged.

During the week following mark-recapture surveys, removal surveys were conducted by replacing live traps with single rat (18 by 8.5 cm; $n = 128$) and mouse (10 by 4.5 cm; $n = 128$) snap traps (McGill Metal Products Co., Marengo, IL). Closed snap traps were placed on each grid a minimum of 3 days prior to the beginning of removal surveys. Each habitat was trapped for 4 consecutive nights, resulting in 1024 trap nights/habitat/WPA. Snap traps were baited with a mixture of peanut butter and oats. Snap traps were checked each morning, and captured animals were examined to determine species, sex, age, and reproductive condition.

Track tubes were constructed, with minor modifications, following the design of Drennan et al. (1998). Two 30-cm-long sections of plastic rain gutter were joined along one edge using duct tape to form an octagonal tube approximately 30 by 12 by 12 cm. The other side of the gutter sections was secured using large binder clips, allowing easy opening of the tube for access to the tracking surface and facilitating transport and storage of the track tubes. The tracking surface consisted of a 20 by 7 cm piece of contact paper, placed with the sticky side facing up, attached to the bottom inside of the track tube using poster putty. Felt ink pads (7 by 4.5 cm) were attached to the floor of the track tube at each end of the contact paper using small binder clips. The location of the ink pads ensured that small mammals traveling through the track tube from either direction would leave ink (a 1:1 mixture of carbon black and paraffin oil) footprints on the contact paper. Track tubes were baited with a small amount of peanut butter and oats smeared onto the ceiling of the track tube.

Track tube surveys were conducted concurrent with mark-recapture surveys, with the exception of a pair of habitats on a single WPA in 2001 that were not surveyed with track tubes. Individual track tubes were placed in the center of each group of 4 Sherman live trap grid locations ($n = 105$ track tubes/habitat). Track tubes were checked each morning and contact paper with evidence of small mammal tracks was removed from track tubes and attached to unlined white paper to retain a permanent record of tracks. Tracks were identified using a reference track collection created using captured small mammals of known species, sex, and weight. In general, tracks could be identified to species; however there was some

difficulty in differentiating between tracks of small meadow voles (*Microtus pennsylvanicus*) and large deer mice (*Peromyscus maniculatus*). Tracks that could not be positively identified as being either meadow vole or deer mouse tracks were classified as “unknown mouse.” In addition, tracks of Franklin’s ground squirrels (*Spermophilus franklinii*) and thirteen-lined ground squirrels (*S. tridecemlineatus*) were difficult to differentiate because of similar track characteristics and size overlap. Therefore, all ground squirrel tracks were combined and classified as “ground squirrel”. When evaluating track tubes, no attempt was made to determine if >1 individual of a species was responsible for tracks within a single track tube. The track tube index was defined as the total number of track tubes with tracks identifiable to species during the 4-night survey period. Under this definition it was possible for a single track tube to be counted multiple times if it recorded tracks on several nights or if it recorded identifiable tracks of >1 species on a single night.

Throughout both field seasons, the time required for all survey activities (e.g., setting traps, monitoring traps and track tubes) was measured and the cost and weight of materials necessary for the implementation of each survey method was determined. The number of technicians participating in survey activities was recorded and used to standardize all time measurements prior to analysis. For the purpose of this study, the most efficient survey method was defined as the method with the minimum implementation time, cost, and weight. All small mammal trapping and handling procedures followed guidelines approved by the American Society of Mammalogists (Animal Care and Use Committee 1998), the Northern Prairie Wildlife Research Center’s Animal Care and Use Guidelines, and the Iowa State University Committee on Animal Care.

Statistical Analysis

Comparison of Mark-Recapture, Removal, and Track Tube Surveys.—Generalized linear models (Proc MIXED, SAS Institute 1999) were used to test for differences in small mammal capture probabilities (\hat{p} , Otis et al. 1978), the number of unique individuals captured or detected (M_{t+1}), and the species richness (S), evenness (E), and diversity (H') detected by mark-recapture, removal, and track tube surveys. For the determination of species richness of track tube surveys, Franklin’s ground squirrels and thirteen-lined ground squirrels were

counted separately if tracks of both species were identified in a habitat, even though ground squirrel tracks were pooled for other analyses. Evenness and diversity were calculated following the methods described by Hayek and Buzas (1997:379). Comparisons between survey methods were first made with models containing all possible interactions between year, habitat, and survey method. Non-significant interactions were removed from models and main effects were interpreted only if there were no significant interactions. If a significant survey method main effect was detected, linear contrasts were used to test for significant differences between each pair of survey methods.

Population Estimation from Mark-Recapture and Removal Surveys.—Population estimates (hereafter, \hat{N} without a subscript refers to population estimates in general) were calculated using models for closed populations in program CAPTURE (Version 6/92; Otis et al. 1978, Rexstad and Burnham 1991). A single estimator was used for each survey method to facilitate comparison between estimates and track tube indices. All population estimates from mark-recapture surveys (hereafter, \hat{N}_{MR}) were calculated using the interpolated jackknife estimator (model M_h in CAPTURE, Otis et al. 1978, Burnham and Overton 1979). The jackknife estimator is relatively robust to variation in the capture probability of individuals (Otis et al. 1978) and provides reasonable population estimates when sampling periods are short or the number of captured individuals is low (Manning et al. 1995). All population estimates from removal surveys (hereafter, \hat{N}_{REM}) were calculated using the generalized removal model (model M_{bh} in CAPTURE, Otis et al. 1978). This estimator is robust to variation in the capture probability of individuals and produces population estimates of low bias (Otis et al. 1978).

Regressions between \hat{N} and Track Tube Indices.—Relationships between \hat{N}_{MR} and \hat{N}_{REM} and track tube indices were investigated using regression analyses (Proc REG, SAS Institute 1999), with \hat{N} as the dependent variable and the track tube index as the independent variable. Regressions were constrained to pass through the origin to allow investigation of the proportionality between \hat{N} and track tube indices (Slade and Blair 2000). Regressions were compared based on coefficients of determination (r^2) and root mean squared errors (RMSE), with greater r^2 values and lesser RMSE indicating the best regression. When regressions are

constrained to pass through the origin, r^2 values are not directly comparable to traditional (i.e., unconstrained) regression r^2 values due to differences in how the model sum of squares are determined in the constrained and unconstrained regressions (P. M. Dixon, Iowa State University Dept. of Statistics, personal communication). To facilitate interpretation and comparison of constrained regression models with unconstrained regression models, corrected r^2 (hereafter, r^2_C) values were calculated as follows:

$$r^2_C = \frac{(\text{Total SS for unconstrained regression} - \text{Error SS for constrained regression})}{\text{Total SS for unconstrained regression}}$$

(P. M. Dixon, Iowa State University Dept. of Statistics, personal communication).

Regressions were weighted by the relative variability of \hat{N} , as measured by the coefficient of variation ($CV(\hat{N})$, Sokal and Rohlf 1995), to account for differences in the precision of \hat{N} for different years and habitats. Each $CV(\hat{N})$ was divided by the median CV value, so that CVs close to the median were assigned scaled values of approximately 1.0. Regression weights were then calculated as the reciprocal of the scaled $CV(\hat{N})$, such that estimates with small $CV(\hat{N})$ received greater weights and had more influence on the regression slope.

Several linear and simple curvilinear models were considered for the relationship between \hat{N} and track tube indices. Curvilinear models that were considered and evaluated in preliminary analyses included a quadratic polynomial, a square root transformation of track tube indices, and a log transformation of track tube indices (Sokal and Rohlf 1995). Preliminary analyses revealed that neither the quadratic polynomial nor the log transformation models adequately reflected the general relationship between \hat{N} and track tube indices. These models predicted that \hat{N} would asymptote or decline (the quadratic polynomial model) as track tube indices increased, which did not seem biologically reasonable. Consequently, although the quadratic polynomial and the log transformation models occasionally yielded r^2 and r^2_C values as high as or slightly higher than other regression models, they were excluded from consideration when determining the best regression between \hat{N} and track tube indices.

Preliminary regression analyses also indicated that ground squirrel tracks tube indices were highly influential in regressions. Trapping grids with high numbers of ground squirrel track tube indices often appeared to be outliers from the general relationship between \hat{N} and track tube indices. Therefore, mark-recapture, removal, and track tube survey data were divided into three subsets for population estimation and regression analyses. The first, “all small mammals,” contained all species captured or detected during mark-recapture, removal surveys, and track tube surveys. The second, “without squirrels,” contained all species except Franklin’s ground squirrels and thirteen-lined ground squirrels. Finally, “vole” contained only meadow vole captures and tracks. The meadow vole was the only species captured in sufficient numbers to allow population estimation across the majority of trapping grids.

Separate regressions were calculated for each habitat and year. Analysis of covariance (ANCOVA, Proc MIXED, SAS Institute 1999) was used to test for equality of regression slopes. All possible main effects, two-way interactions, and the three-way interaction between track tube indices, habitats, and years were tested for significance. Non-significant interactions were removed from consideration in a stepwise fashion, beginning with the three-way interaction. A significant interaction was interpreted as evidence that regression slopes differed and should not be pooled into a combined regression.

Relative Efficiency of Survey Methods.—Generalized linear models (Proc GLM, SAS Institute 1999) were used to determine if there were differences in the time required to complete mark-recapture, removal, and track tube surveys, after accounting for the number of technicians participating in daily surveys. Comparisons were first made with models containing all possible interactions between year, habitat, and survey method. Non-significant interactions were removed from the model and main effects were interpreted only if there were no significant interactions. If a significant survey method main effect was detected, linear contrasts were used to test for significant differences between each pair of survey methods. Equipment cost and weight for each survey method were compared in a qualitative fashion.

RESULTS

Comparison of Mark-Recapture, Removal, and Track Tube Surveys

A total of 1,735 unique individuals of 10 species were captured during 17,408 trap nights of mark-recapture live trapping surveys in 2001 and 2002 (Table 1). Meadow voles were the most commonly captured species in both years and habitats (80.8% of total live captures). Masked shrews (*Sorex cinereus*), thirteen-lined ground squirrels, deer mice, and meadow jumping mice (*Zapus hudsonius*) (ordered in increasing abundance) made up 1.3–6.3% of total live captures (Table 1). During removal snap trapping surveys in 2001 and 2002, a total of 3,758 unique individuals of 10 species were captured in 34,816 trap nights (Table 1). As with live trapping, meadow voles were the most commonly captured species in both years and habitats (76.7% of total snap captures). Franklin's ground squirrels, deer mice, masked shrews, meadow jumping mice, and thirteen-lined ground squirrels (ordered in increasing abundance) made up 1.6–6.8% of total snap captures (Table 1).

Estimated capture probabilities were significantly greater during removal surveys ($\bar{p} = 0.285$, SE = 0.014) than during mark-recapture surveys ($\bar{p} = 0.174$, SE = 0.014, $F = 31.06$, $df = 1, 64$, $P < 0.001$), after controlling for the effects of habitat and year. In comparison to mark-recapture surveys, removal surveys captured significantly more total small mammals ($\overline{M}_{t+1} = 110.53$, SE = 10.04 vs. $\overline{M}_{t+1} = 51.03$, SE = 6.81, $F = 24.37$, $df = 1, 64$, $P < 0.001$), meadow voles ($\overline{M}_{t+1} = 84.83$, SE = 9.87 vs. $\overline{M}_{t+1} = 41.26$, SE = 6.72, $F = 13.97$, $df = 1, 64$, $P < 0.001$), masked shrews ($\overline{M}_{t+1} = 4.53$, SE = 1.24 vs. $\overline{M}_{t+1} = 0.68$, SE = 0.20, $F = 9.94$, $df = 1, 64$, $P = 0.003$), Franklin's ground squirrels ($\overline{M}_{t+1} = 1.82$, SE = 0.54 vs. $\overline{M}_{t+1} = 0.32$, SE = 0.16, $F = 7.05$, $df = 1, 64$, $P = 0.01$), thirteen-lined ground squirrels ($\overline{M}_{t+1} = 7.56$, SE = 1.11 vs. $\overline{M}_{t+1} = 2.18$, SE = 0.41, $F = 21.36$, $df = 1, 64$, $P < 0.001$), and meadow jumping mice ($\overline{M}_{t+1} = 7.18$, SE = 1.59 vs. $\overline{M}_{t+1} = 3.21$, SE = 1.21, $F = 4.31$, $df = 1, 64$, $P = 0.042$), after controlling for the effects of habitat and year (Table 1). Removal surveys also captured more species than mark-recapture surveys ($\bar{S} = 5.00$, SE = 0.27 vs. $\bar{S} = 3.97$, SE = 0.24, $F = 8.27$, $df = 1, 64$, $P = 0.006$), but detected lower evenness ($\bar{E} = 0.48$, SE = 0.02 vs. $\bar{E} = 0.59$, SE = 0.04, $F = 5.99$, $df = 1, 64$, $P = 0.017$), after controlling for the effects of habitat and year

(Table 1). Examination of capture records for the 34 upland and wet-meadow habitats sampled by mark-recapture and removal surveys provides further evidence of possible species-specific bias in capture rates. Masked shrews, Franklin's ground squirrels, and meadow jumping mice were frequently captured during removal surveys, but not during corresponding mark-recapture surveys (Figure 1). In contrast, least weasels (*Mustela nivalis*) and Northern short-tailed shrews (*Blarina brevicauda*) were often captured during mark-recapture surveys, but not removal surveys (Figure 1), although differences in capture rates between mark-recapture and removal surveys were not significant for these species. Even with these apparent species-specific sampling biases, there were significant correlations between the number of captures of the six most commonly captured species during mark-recapture and removal survey ($r_s = 0.387\text{--}0.873$, Table 2).

During track tube surveys in 2001 and 2002, a total of 3,659 track tubes with identifiable tracks of 8 species were recorded in 13,440 track tube nights (Table 1). Often, individual track tubes contained identifiable tracks of >1 species. With the exception of upland habitats in 2002, the most commonly detected species was the meadow vole (46.2% of total track records), although ground squirrel tracks also contributed a large proportion (42.1%) of total track records (Table 1). Tracks identified as belonging to deer mice and meadow jumping mice made up 1.4% and 3.0% of total track records, respectively. Slightly greater than 6% of tracks were identified as being either meadow vole or deer mouse tracks but could not be differentiated between these two species (Table 1).

In comparison to removal surveys, track tube surveys detected fewer species ($\bar{S} = 3.31$, $SE = 0.21$ vs. $\bar{S} = 5.00$, $SE = 0.27$, $F = 24.79$, $df = 1$, 95 , $P < 0.001$), higher evenness ($\bar{E} = 0.64$, $SE = 0.04$ vs. $\bar{E} = 0.48$, $SE = 0.02$, $F = 10.27$, $df = 1$, 95 , $P = 0.002$), and lower diversity ($\bar{H}' = 0.62$, $SE = 0.05$ vs. $\bar{H}' = 0.80$, $SE = 0.07$, $F = 4.45$, $df = 1$, 95 , $P = 0.038$), after controlling for the effects of habitat and year (Table 1). There was moderate evidence that track tube surveys detected fewer species than mark-recapture surveys ($\bar{S} = 3.31$, $SE = 0.21$ vs. $\bar{S} = 3.97$, $SE = 0.24$, $F = 3.88$, $df = 1$, 95 , $P = 0.052$) after controlling for habitat and year (Table 1). Examination of survey records for the 32 sites sampled with all three survey methods provides insight into possible species-specific bias in track tube detection rates.

With the exception of ground squirrels and meadow voles, small mammal species were often not detected by track tube surveys in habitats where they were captured by mark-recapture or removal surveys (Figure 2). In contrast, deer mice and least weasels were detected by track tube surveys in 3 habitats where they were not captured during mark-recapture or removal surveys (Figure 2). Even with these apparent biases in species-specific detection rates, track tube indices were correlated with the number of captures of the six most common species during mark-recapture surveys ($r_s = 0.245\text{--}0.834$, Table 2) and removal surveys ($r_s = 0.302\text{--}0.767$, Table 2).

Relationships between \hat{N} and Track Tube Indices

As expected based on the disparity between the number of individuals captured during mark-recapture and removal surveys, \hat{N}_{REM} were generally greater than \hat{N}_{MR} (Table 3, Appendix). When all captured small mammals are considered (all small mammals), \hat{N}_{REM} was greater than \hat{N}_{MR} on 29 of 33 trapping grids where estimates could be generated from both surveys. When captures of Franklin's ground squirrels and thirteen-lined ground squirrels were excluded (without squirrels), \hat{N}_{REM} was greater than \hat{N}_{MR} on 27 of 32 trapping grids. \hat{N}_{REM} generated exclusively from meadow vole captures (vole) was greater than \hat{N}_{MR} on 24 of 31 trapping grids where estimates could be generated from both surveys. On many trapping grids, \hat{N}_{REM} was 2 or more times greater than \hat{N}_{MR} . Nonetheless, \hat{N}_{MR} and \hat{N}_{REM} were highly correlated ($r = 0.699\text{--}0.764$, Table 4), and track tube indices were correlated with \hat{N}_{MR} ($r_s = 0.601\text{--}0.825$, Table 4) and \hat{N}_{REM} ($r_s = 0.549\text{--}0.596$, Table 4).

Relationships between \hat{N}_{MR} and Track Tube Indices

All small mammals.—The relationship between \hat{N}_{MR} and track tube indices for all species was best fit by the curvilinear square root transformation model in both upland and wet-meadow habitats in 2001 and 2002. Although there was considerable scatter in data points, r^2_{C} values ($\bar{X} = 0.424$, range = 0.228–0.526, Table 5) indicated that a moderate proportion of the variation in \hat{N}_{MR} was explained by variation in track tube indices. Regressions did not differ in slope between habitats (ANCOVA, $F = 2.25$, $df = 1, 28$, $P = 0.145$) but did differ between years (ANCOVA, $F = 6.29$, $df = 1, 28$, $P = 0.018$). Therefore, separate regression equations were produced for each year. When upland and wet-meadow regressions were

combined in 2001, the best-fit regression was curvilinear and had the form $\hat{N}_{MR} = 14.680 (\sqrt{\text{track tube index}})$ (Figure 3A, Table 5). In 2002, the best-fit curvilinear model was $\hat{N}_{MR} = 10.503 (\sqrt{\text{track tube index}})$ (Figure 3B, Table 5). These regressions explained low amounts of the variation in \hat{N}_{MR} ($r^2_C = 0.297$ and 0.404 , respectively, Table 5) and 95% prediction intervals (Figure 3A, B) suggest that these regressions would have low precision when predicting small mammal abundance from new track tube index observations.

Without squirrels.—After the removal of Franklin’s ground squirrel and thirteen-lined ground squirrel captures and track indices, the relationship between \hat{N}_{MR} and track tube indices was best fit by the curvilinear model in upland habitats in 2001 and wet-meadow habitats in 2002, but by the linear model in wet-meadow habitats in 2001 and upland habitats in 2002 (Table 5). After the removal of ground squirrel data, r^2_C values increased ($\bar{X} = 0.603$, range = 0.451 – 0.716 , Table 5). Regression slopes did not differ between habitats (ANCOVA, $F = 2.70$, $df = 1, 28$, $P = 0.112$) but were different between years (ANCOVA, $F = 17.97$, $df = 1, 28$, $P < 0.001$). Therefore, separate regression equations were produced for each year. When upland and wet-meadow regressions were combined in 2001, the best-fit regression was curvilinear and had the form $\hat{N}_{MR} = 18.569 (\sqrt{\text{track tube index}})$ (Figure 3C, Table 5). In 2002, the best-fit linear model was $\hat{N}_{MR} = 1.192 (\text{track tube index})$ (Figure 3D, Table 5). Although these regressions explain a large proportion of the variation in \hat{N}_{MR} ($r^2_C = 0.778$ and 0.711 , respectively; Table 5), 95% prediction intervals (Figure 3C, D) suggest low precision when predicting abundance from new track tube index observations.

Vole.—When only meadow vole captures and track tube indices were included in analyses, the relationship between \hat{N}_{MR} and track tube indices was best fit by the curvilinear model, with the exception of wet-meadow habitats in 2001 where the linear model explained slightly more variation (linear $r^2_C = 0.956$ versus curvilinear $r^2_C = 0.952$). The amount of variation in \hat{N}_{MR} explained by track tube indices was similar to “without squirrels” regressions ($\bar{X} = 0.599$, range = 0.455 – 0.716 , Table 5). Regression slopes did not differ between habitats (ANCOVA, $F = 2.92$, $df = 1, 28$, $P = 0.099$) but were different between years (ANCOVA, $F = 11.26$, $df = 1, 28$, $P = 0.002$). Therefore, separate regression equations were produced for each year. In 2001, the best-fit curvilinear model was $\hat{N}_{MR} = 17.779 (\sqrt{\text{track tube index}})$

(Figure 3E, Table 5). When upland and wet-meadow regressions were combined in 2002, the best-fit curvilinear regression was $\hat{N}_{MR} = 13.152 (\sqrt{\text{track tube index}})$ (Figure 3F, Table 5). These regressions explain a large proportion of the variation in \hat{N}_{MR} ($r^2_C = 0.752$ and 0.691 , respectively; Table 5), but 95% prediction intervals (Figure 3E, F) suggest low precision when predicting abundance from new track tube index observations.

Relationship between \hat{N}_{REM} and Track Tube Indices

All small mammals.—The relationship between \hat{N}_{REM} and track tube indices for all small mammal species was best fit by the curvilinear square root transformation model in both upland and wet-meadow habitats in 2001 and 2002. There was considerable scatter in data points, especially at higher \hat{N} and track tube indices (Figure 4A), and r^2_C values ($\bar{X} = 0.239$, range = 0.000 – 0.519 , Table 6) indicated that variation in track tube indices explained a relatively low proportion of the variation in \hat{N}_{REM} . Regressions did not differ in slope between habitats (ANCOVA, $F = 1.63$, $df = 1, 27$, $P = 0.213$) or years (ANCOVA, $F = 1.64$, $df = 1, 27$, $P = 0.211$). When both habitats and years were combined, the resulting curvilinear regression model was $\hat{N}_{REM} = 13.684 (\sqrt{\text{track tube index}})$ (Figure 4A, Table 6). However, this regression explained little of the variation in \hat{N}_{REM} ($r^2_C = 0.000$, Table 6) and 95% prediction intervals (Figure 4A) suggest low precision when predicting abundance from new track tube index observations.

Without squirrels.—After the removal of Franklin’s ground squirrel and thirteen-lined ground squirrel captures and tracks, the relationship between \hat{N}_{REM} and track tube indices was best fit by the curvilinear model in both upland and wet-meadow habitats in 2001 and 2002. After the removal of ground squirrel data, r^2_C values decreased further ($\bar{X} = 0.179$, range = 0.000 – 0.304 , Table 6), indicating that track tube indices explained even less of the variation in \hat{N}_{REM} . Regression slopes did not differ between habitats (ANCOVA, $F = 2.10$, $df = 1, 27$, $P = 0.123$) or years (ANCOVA, $F = 1.75$, $df = 1, 27$, $P = 0.197$). When both habitats and years were combined, the resulting curvilinear regression model was $\hat{N}_{REM} = 17.062 (\sqrt{\text{track tube index}})$ (Figure 4B, Table 6). This regression explained only a small portion of the variation in \hat{N}_{REM} ($r^2_C = 0.058$, Table 6) and 95% prediction intervals (Figure

4B) suggest low precision when predicting abundance from new track tube index observations.

Vole.—When only meadow vole captures and tracks were included in analyses, the relationship between \hat{N}_{REM} and track tube indices was best fit by the curvilinear model in both upland and wet-meadow habitats in 2001 and 2002. In comparison to “all small mammal” and “without squirrel” regressions, track tube indices explained even less of the variation in \hat{N}_{REM} ($\bar{X} = 0.145$, range = 0.000–0.201, Table 6). Regression slopes did not differ between habitats (ANCOVA, $F = 2.54$, $df = 1, 26$, $P = 0.123$) or years (ANCOVA, $F = 3.11$, $df = 1, 26$, $P = 0.089$). When both habitats and years were combined, the resulting curvilinear regression model was $\hat{N}_{\text{REM}} = 14.598 (\sqrt{\text{track tube index}})$ (Figure 4C, Table 6). This regression explained only a small portion of the variation in \hat{N}_{REM} ($r^2_{\text{C}} = 0.065$, Table 6) and 95% prediction intervals (Figure 4C) suggest low precision when predicting abundance from new track tube index observations.

Relative Efficiency of Survey Methods

Track tubes were relatively lightweight, inexpensive, and quick to set and monitor in the field. Track tubes and Sherman live traps were approximately equal in weight per 100 units (35 kg and 36 kg, respectively), whereas 100 McGill rat traps and 100 mouse traps together weighed only 19 kg. The total cost of a single track tube was approximately \$1.40, whereas Sherman live traps cost approximately \$12.80 per trap, McGill rat traps approximately \$1.50 per trap, and McGill mouse traps \$0.25 – \$0.30 per trap. For an entire grid, these costs equate to approximately \$147 for 105 track tubes, \$1620 for 128 Sherman live traps, and \$230 for 128 McGill rat and 128 mouse traps. After correction for variation in the number of technicians participating in daily surveys, track tube surveys required, on average, 438 (SE = 34.32) minutes/habitat/4-day survey period, whereas mark-recapture surveys required 688 (SE = 54.95) minutes/habitat/4-day survey period and removal surveys required 637 (SE = 21.78) minutes/habitat/4-day survey period. The average time required for track tube surveys was significantly less than mark-recapture surveys ($F = 21.29$, $df = 1, 91$, $P < 0.001$) and removal surveys ($F = 13.46$, $df = 1, 91$, $P < 0.001$). The average time required for mark-recapture and removal surveys was not significantly different ($F = 0.89$, $df = 1, 91$, $P =$

0.347). Light to moderate wind and rain had no effect on track tubes. However, on a few occasions heavy rainfall caused ink to run from the felt ink pads onto the contact paper, which complicated track identification. There was no indication that dry or windy conditions reduced the ability of track tubes to record ink footprints, even after several days in the field. Although the effects of inclement weather on Sherman live traps and McGill snap traps was not specifically tested, increased numbers of closed, empty live and snap traps were observed following nights with high wind and heavy rain. It is likely that the movement of vegetation during high winds or heavy rain events may cause the closure of some traps.

DISCUSSION

Comparison of Mark-Recapture, Removal, and Track Tube Surveys

Mark-recapture, removal, and track tube surveys produced qualitatively and quantitatively different conclusions about the abundance and diversity of small mammals on sampled areas. On a trapping grid specific basis, removal surveys consistently detected more small mammal species, and captured more individuals of those species, than mark-recapture surveys. An obvious explanation for this discrepancy is that twice as many traps were present during removal surveys, suggesting that traps may have been limiting during mark-recapture surveys. Alternatively, it may be that differences in the design of live and snap traps influence capture probabilities for some species or individuals. The enclosed design of live traps may be avoided during foraging activities, while the open design of snap traps may not cause an avoidance response. Shrews are known to have low capture rates in live traps, either because of avoidance or perhaps because they do not weigh enough to trigger the traps. In fact, protocols for sampling shrews generally recommend snap traps, pitfall traps, or some combination of the two (Jones et al. 1996). Ground squirrels may have been captured less frequently during mark-recapture surveys because their large size makes it less likely that they will enter and be captured in Sherman traps. It is also possible that the presence of baited Sherman traps during the week preceding removal surveys may have attracted small mammals from the surrounding habitat. The removal of small mammals from sampled habitats may have resulted in invasion by individuals from surrounding areas, thereby

violating the assumption of closure (Otis et al. 1978). However, it seems unlikely that closure would be violated in the short duration surveys used in this study.

In general, species commonly captured during mark-recapture and removal surveys were detected by track tube surveys and species rarely captured during mark-recapture and removal surveys were rarely or never detected by track tube surveys. However, ground squirrels were overrepresented and meadow voles were underrepresented in track tube surveys in comparison to mark-recapture and removal survey capture rates. Because it is difficult and time consuming to identify individual small mammals from footprint characteristics (Justice 1961, Sheppe 1965, Van Apeldoorn et al. 1993, Zielinski and Truex 1995), it is not clear whether individual or species-specific behavior explains differences in track tube detection rates. It is interesting to note that if ground squirrel tracks are removed from consideration, detection rates of meadow voles (79.8% of remaining track tubes with tracks), deer mice (2.4%), and meadow jumping mice (5.1%) are very similar to capture rates of these species during mark-recapture and removal surveys. This suggests that track tube detection rates of commonly captured species, with the exception of ground squirrels, are approximately proportional to capture rates during mark-recapture and removal surveys. The influential effects of ground squirrels on track tube indices are most likely related to home range size. Thirteen-lined ground squirrels typically have home ranges of 1–4 ha (McCarley 1966), whereas other small mammal species sampled during this study have home ranges <0.05–0.5 ha (Quimby 1951, Van Vleck 1969), suggesting that ground squirrels may have the opportunity to visit more track tubes per night than other species. In the case of small species, such as shrews, it is possible that some tracks were missed on track sheets containing tracks of multiple species or tracks of larger species such as meadow voles or ground squirrels.

Relationships between \hat{N} and Track Tube Indices

Track tube indices were relatively poor predictors of \hat{N} . Both curvilinear and linear regression models best fit data for different habitat and year combinations, suggesting inconsistency in the relationship between \hat{N} and track tube indices. In several cases, the slope of predictive regressions differed between years, providing further evidence of a lack of

generality or consistency in the relationship between \hat{N} and track tube indices. Most importantly, the wide 95% prediction intervals for a new track tube index observation indicate poor precision when utilizing the track tube index to predict \hat{N} .

In general, regressions between \hat{N}_{MR} and track tube indices had higher r^2_C values than regressions between \hat{N}_{REM} and track tube indices, suggesting a stronger or more consistent relationship between \hat{N}_{MR} and track tube indices. It is possible that the relationship between \hat{N}_{MR} and track tube indices results from similar responses of small mammals to the enclosed design of Sherman traps and track tubes. Ground squirrel tracks had a large effect on the slope and goodness of fit of regressions between \hat{N} and track tube indices; removing ground squirrel data from track tube indices generally improved the fit of regressions. The influence of ground squirrels on track tube surveys suggests that it might be advantageous to modify track tube surveys to limit exposure to ground squirrels. One method might be to decrease the diameter of track tubes, although track tubes sized to exclude ground squirrels might also be utilized differently by other species. Another possibility would be to make track tubes unavailable during the daytime, as ground squirrels are diurnal whereas most other common small mammal species are nocturnal. However, additional daily manipulation of track tubes would decrease any advantages in monitoring time that track tube surveys have over mark-recapture and removal surveys.

Intuitively, the strongest relationship between \hat{N} and track tube indices should occur when only a single species is considered. However, regressions involving only meadow vole data did not have the best fit for either \hat{N}_{MR} or \hat{N}_{REM} regressions. Two recent studies of track tube surveys have reported strong correlations between estimates or indices of abundance and track tube indices (Drennan et al. 1998, Glennon et al. 2002). Drennan et al. (1998) found strong correlations between abundance and track tube indices of 6 sciurids. Glennon et al. (2002) also reported strong correlations between abundance and track indices of small mammals, although no measure of the predictive ability of these relationships was provided. As in my research, a single species (Eastern chipmunk, *Tamias striatus*) was captured in much greater numbers than other species (Glennon et al. 2002). Unlike my surveys, Eastern chipmunks were also the most common species detected in track tube

surveys, which likely explains the improved fit of the Glennon et al. (2002) regressions in comparison to my regressions.

My results provide evidence that the relationship between \hat{N} and track tube indices is not consistent across space and time. A number of possible modifications might improve the predictive capability of track tube index regressions. First, instead of measuring track tube indices as the presence/absence of a species in a track tube, it might be possible to quantify the number of intrusions of individuals in each tube (Engeman et al. 2000). Second, morphometric analyses of small mammal track characteristics (Van Apeldoorn et al. 1993) might improve our ability to identify tracks to species and to differentiate between tracks of individuals (Taylor and Raphael 1988, Van Apeldoorn et al. 1993, Zielinski and Truex 1995). A final modification of track tube surveys that should be tested involves removing bait from track tubes. This might decrease the overabundance of ground squirrel tracks in track tubes, thereby indirectly improving the detection and identification of tracks of other species. However, it is also possible that small mammal response to unbaited track tubes might be uniformly low or might decline quickly after initial explorations (Sheppe 1965).

Efficiency of Survey Methods

Compared to mark-recapture and removal surveys, track tube surveys were significantly faster to set up and monitor in the field and cheaper to implement. However, these time savings may be lost during the data processing stage, depending upon the skill level and experience of the person identifying tracks, the specificity of identification desired, and the number of tracks on each track sheet. Identification of small mammal tracks requires somewhat specialized experience and care must be taken not to miss tracks of small species interspersed with tracks of large species. Unless track identification techniques (e.g., categorizing intrusions, morphometric analyses) provide vast improvements in the identification of similar species and the differentiation of individuals, the increased time requirement associated with more specific identification would offset any possible advantages in terms of cost and labor that track tube surveys have over mark-recapture and removal surveys.

However, there are benefits to using track tube surveys. Track tube surveys have less effect on the small mammal community than mark-recapture or removal surveys. Although mark-recapture survey protocols attempt to minimize mortalities, some small mammals do die in traps and repeated live captures can have detrimental effects on growth and survival rates (Slade 1991). Removal surveys may lead to shifts in the abundance and dominance of species within the small mammal community (Sullivan et al. 2003). If researchers are working with species of conservation concern, or studying community interactions, these shifts could confound true patterns and lead to incorrect conclusions. Finally, track tube surveys decrease the risk of exposure to mammalian-transmitted diseases by eliminating the handling of small mammals.

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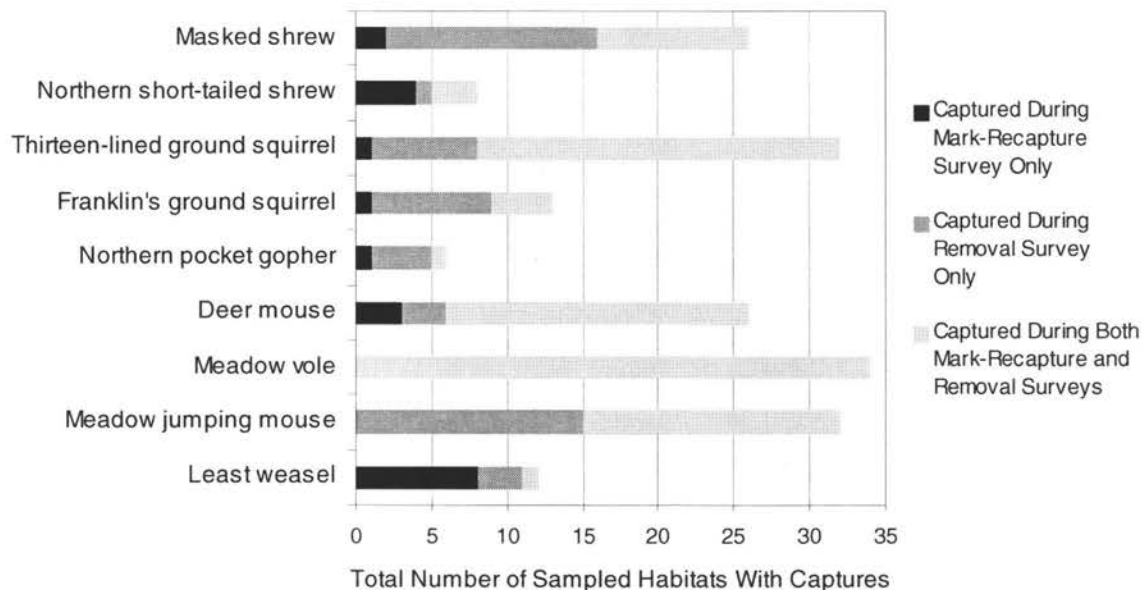


Figure 1. Number of upland and wet-meadow habitats where small mammal species were captured during mark-recapture and removal surveys on Waterfowl Production Areas in Stutsman County, ND, 2001-2002. A total of 34 upland and wet-meadow habitats were surveyed with both mark-recapture and removal surveys.

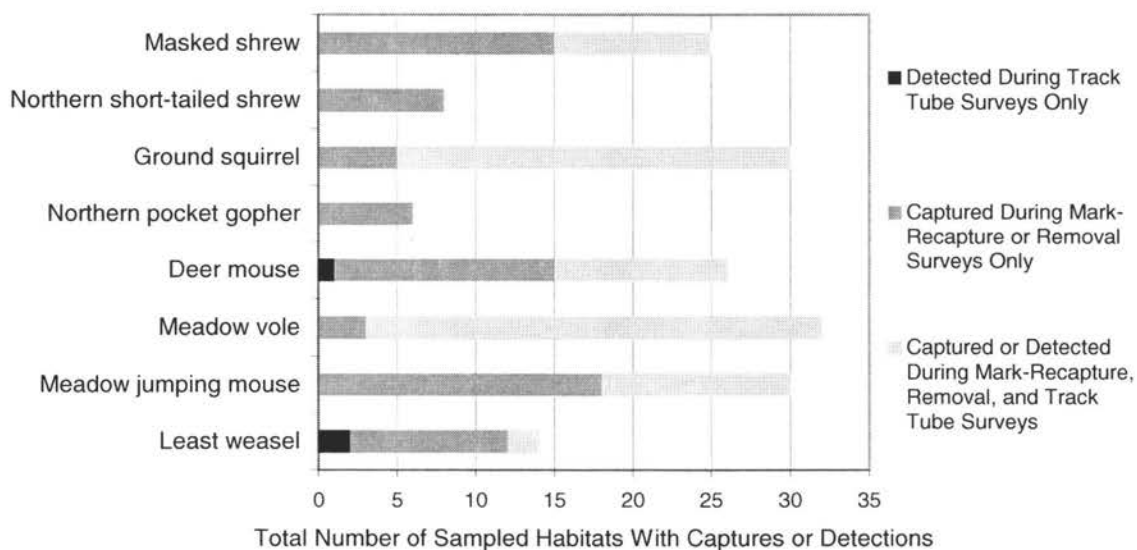
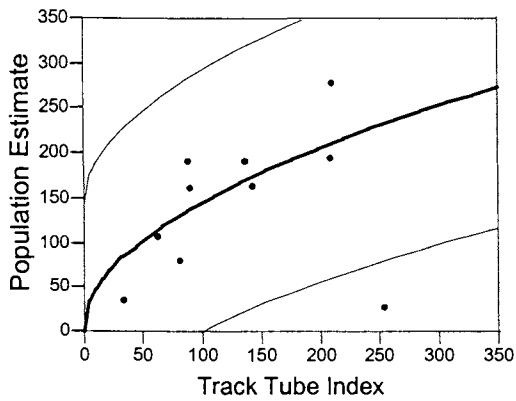
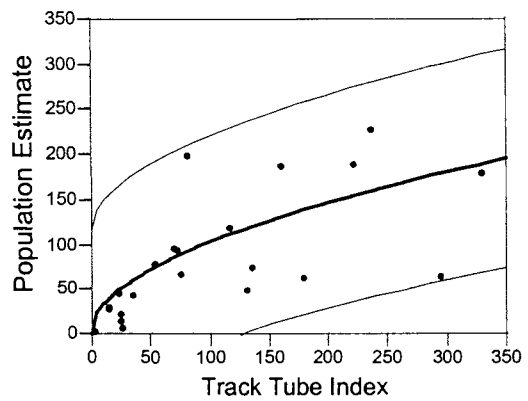


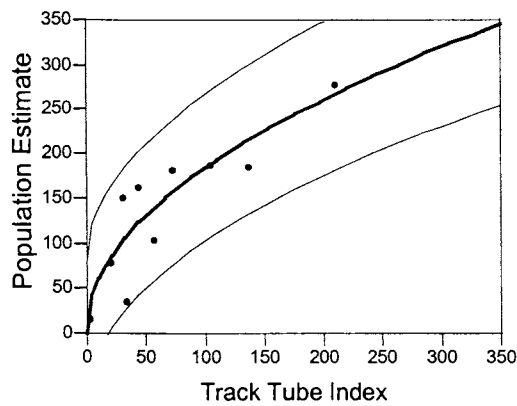
Figure 2. Number of upland and wet-meadow habitats where small mammal species were captured during mark-recapture and removal surveys and detected during track tube surveys on Waterfowl Production Areas in Stutsman County, ND, 2001-2002. A total of 32 upland and wet-meadow habitats were surveyed with all three methods.



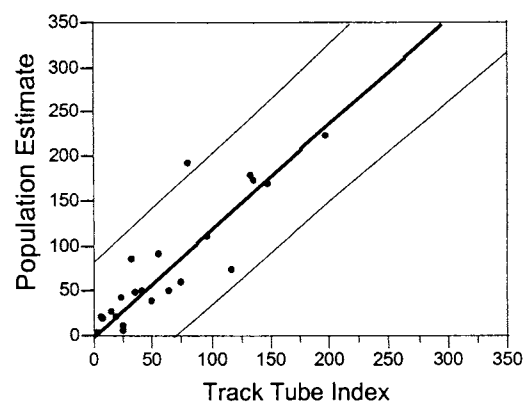
A) All small mammals, 2001



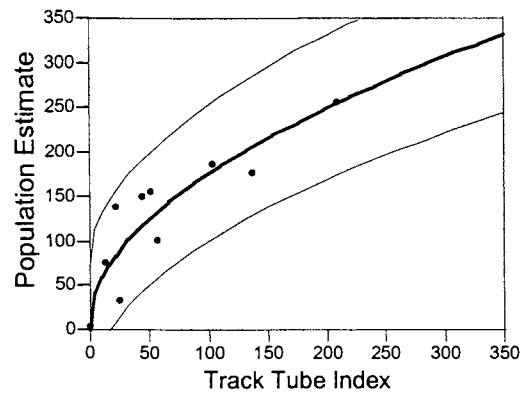
B) All small mammals, 2002



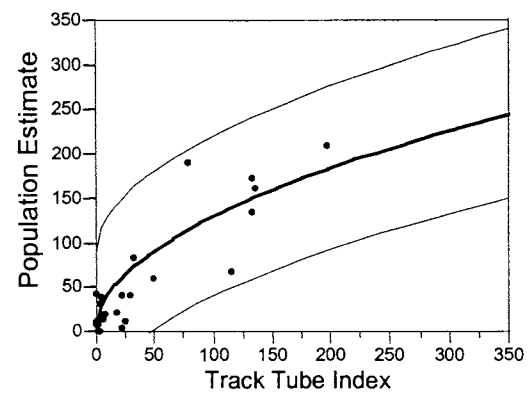
C) Without squirrels, 2001



D) Without squirrels, 2002

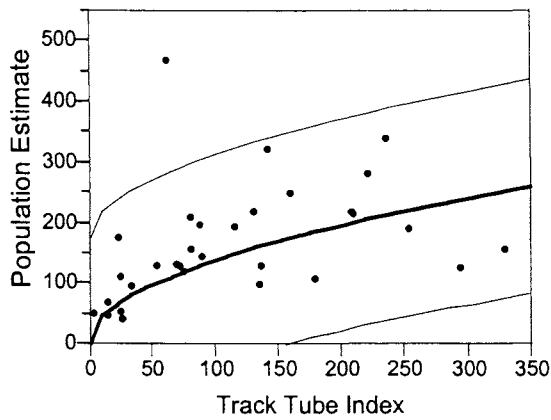


E) Vole, 2001

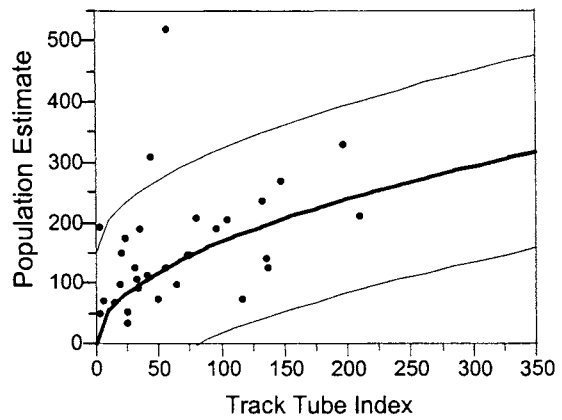


F) Vole, 2002

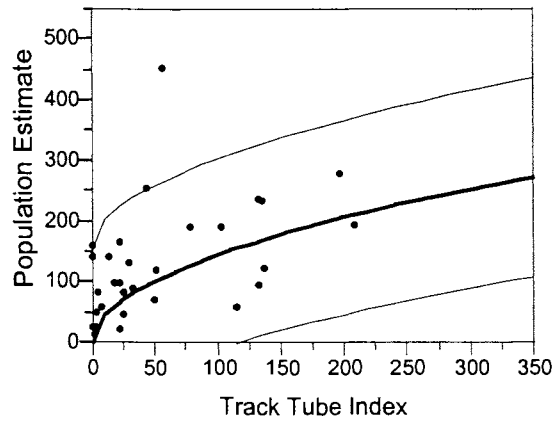
Figure 3. Regressions predicting mark-recapture survey population estimates (\hat{N}_{MR}) as a function of track tube indices for all small mammals (A, B), without squirrels (C, D), and exclusively for captured meadow voles (E, F). Regression lines are indicated in bold and 95% prediction intervals for new track tube index observations are indicated by the lighter lines. Small mammal data were collected on Waterfowl Production Areas in Stutsman County, ND, 2001-2002.



A) All small mammals



B) Without squirrels



C) Vole

Figure 4. Regressions predicting removal survey population estimates (\hat{N}_{REM}) as a function of track tube indices for all small mammals (A), without squirrels (B), and exclusively for captured meadow voles (C). Regression lines are indicated in bold and 95% prediction intervals for new track tube index observations are indicated by the lighter lines. Small mammal data were collected on Waterfowl Production Areas in Stutsman County, ND, 2001-2002.

Table 1. Number of unique individuals captured (M_{t+1}) during mark-recapture and removal surveys and number of track tubes with identifiable tracks (track tube index) during track tube surveys on 1.05 ha grids in upland and wet-meadow habitats on Waterfowl Production Areas in Stutsman County, ND, 2001-2002. Number of sampled grids (n) indicated for each year and habitat.

Species	2001						2002						Years and Habitats Combined		
	Upland n = 8 ^a			Wet Meadow n = 4 ^a			Upland n = 11			Wet Meadow n = 11			Years and Habitats Combined		
	Mark-Recap.	Removal	Track Tube	Mark-Recap.	Removal	Track Tube	Mark-Recap.	Removal	Track Tube	Mark-Recap.	Removal	Track Tube	Mark-Recap.	Removal	Track Tube
Masked shrew (<i>Sorex cinereus</i>)	2	11			8		14	87	22	7	48	12	23	154	34
Northern short-tailed shrew (<i>Blarina brevicauda</i>)	4	2					3	3		2	2		9	7	
Thirteen-lined ground squirrel (<i>Spermophilus tridecemlineatus</i>)	15	52	339 ^b	6	26	258 ^b	33	112	411 ^b	18	67	531 ^b	72	257	1,539 ^b
Franklin's ground squirrel (<i>Spermophilus franklinii</i>)	3	27			3		5	15		3	17		11	62	
Northern pocket gopher (<i>Thomomys talpoides</i>)	2			1	1			3			2		3	6	
Western harvest mouse (<i>Reithrodontomys megalotis</i>)							1						1		
Deer mouse (<i>Peromyscus maniculatus</i>)	18	36	37	6	7	3	40	56	7	29	41	4	93	140	51
Meadow vole (<i>Microtus pennsylvanicus</i>)	477	829	401	188	379	268	263	638	363	475	1,038	660	1,403	2,884	1,692
House mouse (<i>Mus musculus</i>)											2	2		2	2
Meadow jumping mouse (<i>Zapus hudsonius</i>)	8	26	9	13	18		16	57	21	72	141	78	109	242	108
Least weasel (<i>Mustela nivalis</i>)	1				1		4	2		6	1	5	11	4	5
Unknown Mouse ^c									142			86			228
Unidentifiable Species		7	54		4	25		3	46		15	57		29	182
Total ^d	530	990	840	214	447	554	379	976	1,012	612	1,374	1,435	1,735	3,758	3,659

^a Track surveys conducted on 7 upland and 3 wet-meadow habitats in 2001.

^b Tracks of thirteen-lined ground squirrels and Franklin's ground squirrels combined.

^c Tracks of either meadow voles or deer mice.

^d Excluding Unidentifiable Species.

Table 2. Spearman correlation (r_s) between the number of unique individuals captured (M_{t+1}) during mark-recapture and removal surveys, mark-recapture survey M_{t+1} and track tube indices, and removal survey M_{t+1} and track tube indices for six small mammal species commonly captured on 1.05 ha grids in upland and wet-meadow habitats on Waterfowl Production Areas in Stutsman County, ND, 2001-2002.

Species	Mark-Recapture M_{t+1} vs. Removal M_{t+1} ^a		Mark-Recapture M_{t+1} vs. Track Tube Indices ^b		Removal M_{t+1} vs. Track Tube Indices ^b	
	r_s	P	r_s	P	r_s	P
Masked shrew (<i>Sorex cinereus</i>)	0.468	0.005	0.473	0.006	0.476	0.006
Thirteen-lined ground squirrel (<i>Spermophilus tridecemlineatus</i>)	0.608	< 0.001	0.534 ^c	0.002	0.767 ^c	< 0.001
Franklin's ground squirrel (<i>Spermophilus franklinii</i>)	0.514	0.002				
Deer mouse (<i>Peromyscus maniculatus</i>)	0.871	< 0.001	0.245	0.177	0.302	0.093
Meadow vole (<i>Microtus pennsylvanicus</i>)	0.873	< 0.001	0.834	< 0.001	0.743	< 0.001
Meadow jumping mouse (<i>Zapus hudsonius</i>)	0.387	0.024	0.509	0.003	0.455	0.009

^a df = 34

^b df = 32

^c Thirteen-lined ground squirrel and Franklin's ground squirrel M_{t+1} and track tube indices combined.

Table 3. Mean number of unique individuals captured (M_{t+1}), population estimates (\hat{N}), and track tube indices for small mammal species captured on 1.05 ha grids in upland and wet-meadow habitats on Waterfowl Production Areas in Stutsman County, ND, 2001-2002. Sample size (n) indicates the number of sampled grids in each year-habitat combination.

	Year	Habitat	n	Mark-Recapture Surveys				Removal Surveys				Track Tube Surveys	
				\overline{M}_{t+1}	SE	\hat{N}_{MR}	SE	\overline{M}_{t+1}	SE	\hat{N}_{REM}	SE	Track Index	SE
All small mammals	2001	Upland	8	66.3	13.9	155.3	20.6	123.8	18.4	154.1	26.5	112.4	21.3
		Wet Meadow	4	53.5	32.0	166.8	63.8	111.8	28.3	234.1	54.9	176.3	57.5
	2002	Upland	11	34.5	7.4	81.2	16.0	88.7	17.1	139.0	25.8	87.8	21.2
		Wet Meadow	11	55.6	12.7	145.0	21.7	125.0	20.3	181.0	19.9	125.1	34.9
	Years and Habitats Combined		34	51.0	6.8	131.7	13.0	111.4	10.1	164.8	13.2	114.3	15.7
Without squirrels	2001	Upland	8	63.6	13.5	149.3	19.6	113.9	16.9	144.1	23.6	63.9	16.5
		Wet Meadow	4	51.8	32.7	176.7	63.7	104.0	31.1	251.8	74.5	90.3	61.9
	2002	Upland	11	30.6	7.0	71.3	14.8	76.7	15.8	120.3	25.9	50.5	13.8
		Wet Meadow	11	53.2	12.7	140.1	21.7	117.1	19.6	169.4	20.6	76.4	18.2
	Years and Habitats Combined		34	48.2	6.8	127.0	13.0	101.7	9.8	152.9	13.6	66.0	9.9
Vole	2001	Upland	8	59.6	13.3	141.4	18.3	103.6	15.6	127.0	20.6	57.3	17.6
		Wet Meadow	4	47.0	31.2	181.2	52.3	94.8	31.0	233.1	68.7	89.3	62.1
	2002	Upland	11	23.9	7.3	66.1	15.9	58.0	15.8	89.8	23.4	33.0	14.4
		Wet Meadow	11	43.2	12.5	125.6	23.5	94.5	20.2	142.4	22.1	60.0	20.2
	Years and Habitats Combined		34	41.3	6.7	120.2	12.8	84.9	9.9	124.9	13.3	52.9	10.7

Table 4. Pearson correlation (r) between mark-recapture and removal survey population estimates (\hat{N}_{MR} and \hat{N}_{REM} , respectively), Spearman correlation (r_s) between \hat{N}_{MR} and track tube indices, and Spearman correlation (r_s) between \hat{N}_{REM} and track tube indices for small mammal species captured on 1.05 ha trapping grids in upland and wet-meadow habitats on Waterfowl Production Areas in Stutsman County, ND, 2001-2002.

	\hat{N}_{MR} vs. \hat{N}_{REM}			\hat{N}_{MR} vs. Track Tube Indices			\hat{N}_{REM} vs. Track Tube Indices		
	r	df	P	r_s	df	P	r_s	df	P
All small mammals	0.706	29	< 0.001	0.601	31	< 0.001	0.596	29	< 0.001
Without squirrels	0.699	25	0.001	0.825	31	< 0.001	0.549	25	0.005
Vole	0.764	25	< 0.001	0.819	30	< 0.001	0.585	25	0.002

Table 5. Slope estimate (β) and goodness of fit measures for regressions between mark-recapture survey population estimates (\hat{N}_{MR}) and track tube indices for small mammal species captured on 1.05 ha trapping grids in upland and wet-meadow habitats on Waterfowl Production Areas in Stutsman County, ND, 2001-2002. All regressions were constrained to pass through the origin. Corrected r^2 (r_c^2) values are presented to allow comparison of goodness of fit with unconstrained regressions.

	Year	Habitat	Best-fit Model ^a	β	SE	df	RMSE	r^2	r_c^2 ^b
All small mammals	2001	Upland	Curvilinear	14.822	1.249	7	115.698	0.959	0.526
		Wet Meadow	Curvilinear	14.421	5.172	3	354.739	0.795	0.134
		Habitats Combined	Curvilinear	14.680	1.667	10	192.204	0.896	0.297
	2002	Upland	Linear	0.701	0.087	11	97.773	0.866	0.519
		Wet Meadow	Curvilinear	11.646	1.492	11	175.810	0.859	0.228
		Habitats Combined	Curvilinear	10.503	0.989	22	147.276	0.843	0.404
Without squirrels	2001	Upland	Curvilinear	18.609	1.696	7	118.494	0.853	0.451
		Wet Meadow	Linear	1.353	0.068	3	55.249	0.995	0.976
		Habitats Combined	Curvilinear	18.569	1.141	10	104.583	0.967	0.778
	2002	Upland	Linear	0.971	0.107	11	75.875	0.892	0.641
		Wet Meadow	Curvilinear	14.914	1.139	11	105.762	0.945	0.716
		Habitats Combined	Linear	1.192	0.079	22	100.883	0.917	0.711
Vole	2001	Upland	Curvilinear	18.274	1.681	7	110.726	0.952	0.455
		Wet Meadow	Linear	1.253	0.077	3	61.396	0.993	0.956
		Habitats Combined	Curvilinear	17.779	1.101	10	96.704	0.967	0.752
	2002	Upland	Curvilinear	10.201	1.313	10	78.344	0.870	0.626
		Wet Meadow	Curvilinear	14.699	1.246	9	102.731	0.946	0.716
		Habitats Combined	Curvilinear	13.152	1.001	19	101.911	0.906	0.691

^a Candidate models for regressions were linear: $\hat{N} = \beta$ (track tube indices) and curvilinear: $\hat{N} = \beta (\sqrt{\text{track tube indices}})$.

^b $r_c^2 = \frac{(\text{Total SS for unconstrained regression} - \text{Error SS for constrained regression})}{\text{Total SS for unconstrained regression}}$.

Table 6. Slope estimate (β) and goodness of fit measures for regressions between removal survey population estimates (\hat{N}_{REM}) and track tube indices for small mammal species captured on 1.05 ha trapping grids in upland and wet-meadow habitats on Waterfowl Production Areas in Stutsman County, ND, 2001-2002. All regressions were constrained to pass through the origin. Corrected r^2 (r_c^2) values are presented to allow comparison of goodness of fit with unconstrained regressions.

	Year	Habitat	Best-fit Model ^a	β	SE	df	RMSE	r^2	r_c^2 ^b
All small mammals	2001	Upland	Curvilinear	16.314	2.162	7	178.718	0.905	0.197
		Wet Meadow	Curvilinear	16.152	6.633	3	331.327	0.748	0.000
	2002	Upland	Curvilinear	13.987	1.669	10	160.095	0.886	0.519
		Wet Meadow	Curvilinear	12.431	2.079	11	304.716	0.781	0.000
	Years and Habitats Combined		Curvilinear	13.684	1.179	31	235.756	0.818	0.000
Without squirrels	2001	Upland	Curvilinear	17.459	3.829	7	257.220	0.776	0.000
		Wet Meadow	Curvilinear	17.282	8.351	3	366.512	0.682	0.000
	2002	Upland	Curvilinear	15.096	2.550	10	180.739	0.796	0.304
		Wet Meadow	Curvilinear	17.809	1.866	11	188.875	0.901	0.234
	Years and Habitats Combined		Curvilinear	17.062	1.436	31	211.526	0.825	0.058
Vole	2001	Upland	Curvilinear	16.924	3.485	7	223.484	0.797	0.000
		Wet Meadow	Curvilinear	16.032	7.781	3	332.333	0.680	0.000
	2002	Upland	Curvilinear	12.002	2.654	9	200.758	0.719	0.201
		Wet Meadow	Curvilinear	14.866	2.400	9	239.895	0.828	0.089
	Years and Habitats Combined		Curvilinear	14.598	1.530	28	225.147	0.771	0.065

^a Candidate models for regressions were linear: $\hat{N} = \beta$ (track tube indices) and curvilinear: $\hat{N} = \beta (\sqrt{\text{track tube indices}})$.

^b $r_c^2 = \frac{(\text{Total SS for unconstrained regression} - \text{Error SS for constrained regression})}{\text{Total SS for unconstrained regression}}$.

CHAPTER 3: PREDICTING SMALL MAMMAL ABUNDANCE, DIVERSITY, AND DISTRIBUTION IN NORTH DAKOTA GRASSLANDS

A paper to be submitted to the Journal of Mammalogy

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ABSTRACT

Small mammal–habitat associations have been little studied in the grassland–wetland landscapes of the Northern Great Plains. I conducted removal (snap trapping) surveys in 19 upland and 15 wet-meadow habitats in Waterfowl Production Areas in central North Dakota. I developed regression models to predict the number of small mammal captures (\overline{M}_{t+1}) and species diversity in upland and wet-meadow habitats (macrohabitat models) and the distribution of small mammal captures within these habitats (microhabitat models) as a function of soil moisture and vegetation characteristics. Meadow voles (*Microtus pennsylvanicus*) were the most commonly captured species in both upland (75.0% of individuals captured) and wet-meadow (78.6% of individuals captured) habitats. Other commonly captured species included masked shrews (*Sorex cinereus*) in upland habitats, meadow jumping mice (*Zapus hudsonius*) in wet-meadow habitats, and thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*) in both habitats. Overall, more meadow voles ($\overline{M}_{t+1} = 94.5$, SE = 16.4) and more total small mammals ($\overline{M}_{t+1} = 120.1$, SE = 16.0) were captured in wet-meadow habitats than in upland habitats ($\overline{M}_{t+1} = 77.2$, SE = 12.2; $\overline{M}_{t+1} = 102.9$, SE = 12.9, respectively). Macrohabitat predictive models explained 25–74% of the variation in the number of individuals of different species captured and 76% of the variation in species diversity in upland and wet-meadow habitats. Predictive variables common to multiple macrohabitat models included soil moisture, percent forb vegetation, percent litter, and litter depth. Microhabitat regression models explained only 5–15% of the variation in the distribution of small mammal captures within upland and wet-meadow habitats. Predictive variables common to multiple microhabitat models included soil moisture, Robel visual obstruction, vegetation height, and litter depth. These results indicate that in grassland habitats in the Northern Great Plains, small mammals respond most strongly to soil moisture

and vegetation characteristics at the macrohabitat level. The lack of a strong microhabitat-level response to soil and vegetation characteristics may be partially explained by historical land use and current management practices which often decrease microhabitat-level heterogeneity in grasslands.

INTRODUCTION

Small mammal–habitat associations have been extensively studied to better understand such broad-ranging subjects as conservation biology, population dynamics, community ecology, source-sink dynamics, and predator-prey interactions. Studies in a variety of habitats, including forests (Dueser and Shugart 1978; Morris 1984, 1987; Bellows et al. 2001a; McShea et al. 2003), old fields (Morris 1987; Bellows et al. 2001a, b), deserts (Kotler and Brown 1988, Jorgensen and Demarais 1999, Cramer and Willig 2002), and grasslands (Birney et al. 1976; Morris 1984, 1987; Snyder and Best 1988) have concluded that the abundance, diversity, and distribution of small mammals are influenced by habitat features at multiple scales. More specifically, these studies have shown that the availability and quality of food and cover resources (Birney et al. 1976, McShea et al. 2003), patch size and level of fragmentation (Cramer and Willig 2002, McShea et al. 2003), and dominant vegetation (Morris 1984, 1987; Snyder and Best 1988; Bellows et al. 2001a) influence small mammal abundance, diversity, and distribution at the macrohabitat level. At the microhabitat level, small-scale patterns and heterogeneity of these characteristics influence the abundance, diversity, and distribution of small mammal species within macrohabitats (Dueser and Shugart 1978, Morris 1984, Snyder and Best 1988, Bellows et al. 2001b, Cramer and Willig 2002, McShea et al. 2003).

Despite their importance to the grassland–wetland landscapes of the Northern Great Plains, small mammal–habitat associations are less well studied therein. This region serves as the primary breeding ground for numerous grassland- and wetland-associated passerine (Winter and Faaborg 1999, Herkert et al. 2003) and waterfowl species (Greenwood et al. 1995, Beauchamp et al. 1996), many of which have experienced long-term population declines. These population declines have been linked to the combined effects of habitat loss and fragmentation and increased predation pressure by medium-sized predators that have

resulted from anthropogenic landscape changes associated with agriculture (Higgins 1977, Sugden and Beyersbergen 1984, Cowardin et al. 1985, Klett et al. 1988, Sargeant and Raveling 1992, Greenwood et al. 1995, Beauchamp et al. 1996). Many researchers have suggested that small mammals may serve as alternate prey for medium-sized predators and buffer predation of ground- and shrub-nesting birds and their eggs (Byers 1974, Weller 1979, Pehrsson 1986, Beintema and Muskens 1987, Marcstrom et al. 1988, Ackerman 2002). Alternatively, abundant small mammal populations may lead to increased predation pressure on nesting birds and their eggs as predators shift foraging activities to areas where small mammals are abundant or predator population levels increase in response to greater prey availability (Roseberry and Klimstra 1970, Klimstra and Roseberry 1975, Greenwood et al. 1998, Wilson and Bromley 2001).

Although the idea of alternate or buffer prey is not new (e.g., Leopold 1933), there are few definitive conclusions about the role of small mammal populations in the complex community context of predator-prey relationships in general, or specifically in the Northern Great Plains. Improved knowledge of small mammal macrohabitat and microhabitat associations would be an important step in understanding how the small mammal community utilizes grassland patches. Previous research has indicated a number of common associations between grassland soil moisture and vegetation characteristics and small mammal abundance and diversity. For example, numerous studies have reported that meadow voles (*Microtus pennsylvanicus*) prefer moist areas with dense vegetation that provides food resources and protection from predators (Getz 1961a, 1970, 1971; Birney et al. 1976; Grant et al. 1977; Abramsky et al. 1979; Snyder and Best 1988). Similarly, Franklin's ground squirrels (*Spermophilus franklinii*) and meadow jumping mice (*Zapus hudsonius*) prefer dense, grassy cover and are often found in dense vegetation along wetland edges (Getz 1961c, Erlien and Tester 1984). In contrast, other common grassland species, including deer mice (*Peromyscus maniculatus*) and thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*), generally prefer drier, more open habitats (Grant et al. 1977, Abramsky et al. 1979, Snyder and Best 1988, Clark et al. 1989).

Further investigation of small mammal–habitat associations would increase our understanding of how small mammals utilize grassland patches, thereby aiding in further study of the role of small mammals in predator-prey relationships in the Northern Great Plains. My research objectives were: 1) to investigate macrohabitat and microhabitat associations of small mammal species in grassland habitats likely to be used by nesting waterfowl and foraging predators; 2) to develop regression models predicting small mammal abundance and diversity as a function of soil moisture and vegetation characteristics at the macrohabitat level; and 3) to develop logistic regression models predicting the distribution of small mammals as a function of soil moisture and vegetation characteristics at the microhabitat level.

STUDY AREA

Fieldwork was conducted on federally owned Waterfowl Production Areas (WPAs) in the Missouri Coteau physiographic region in western Stutsman County, North Dakota, between May and August, 2001-2002. The Missouri Coteau, a geologic formation extending from east-central South Dakota through southwestern Saskatchewan, is an area of rugged morainic hills rising 91-152 m above the adjacent Drift Plain (Euliss 1996). The native vegetation of the Missouri Coteau in central North Dakota is mixed-grass prairie dominated by western wheatgrass (*Agropyron smithii*), needle and thread (*Hesperostipa comata*), big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), green needlegrass (*Nassella viridula*), prairie cordgrass (*Spartina pectinata*), and northern reedgrass (*Calamagrostis stricta*), and also containing a diverse mix of forbs such as Maximilian sunflower (*Helianthus maximiliani*) and Canada goldenrod (*Solidago canadensis*) (Euliss 1996). WPAs may contain native prairie remnants, although most are formerly cultivated or grazed areas that have been planted to native grasses, non-native cool-season grasses, or dense nesting cover (Duebbert and Lokemoen 1976). WPA management practices consist of burning, fertilization, grazing, scarification, or mowing, depending on land-use history and specific management goals (Euliss 1996).

METHODS

Small Mammal Surveys

Small mammal surveys were conducted on randomly selected WPAs between mid-May and early-August 2001 ($n = 5$) and 2002 ($n = 8$). To be considered for study, WPAs had to be ≥ 16 ha in area and contain at least one seasonal or semi-permanent wetland ≥ 3 ha in size. WPAs mowed or burned < 1 year prior to the beginning of each field season were not considered. On each selected WPA, upland and wet-meadow habitats were identified using aerial photographs and ground-truthing. Paired upland and wet-meadow habitats, separated by ≥ 300 m to minimize the likelihood of small mammal dispersal between habitats, were selected for small mammal surveys. Selected WPAs were large (approximately 100–600 ha) and often contained multiple upland and wet-meadow habitat pairs suitable for this study. As a result, 2 pairs of upland and wet-meadow habitats were surveyed on 1 WPA in 2001 and 3 WPAs in 2002. Heavy spring and summer rains during the 2001 field season flooded all suitable wet-meadow habitats on 3 WPAs; additional upland habitats were selected for sampling in these situations. In total, 8 upland and 4 wet-meadow habitats were surveyed in 2001, and 11 upland and 11 wet-meadow habitats were surveyed in 2002 (Appendix).

Within each paired upland and wet-meadow habitat, a single 8 by 16 trapping grid (10 m between trap locations, $n = 128$ trap locations, total area = 1.05 ha) was established. Rectangular trapping grids were chosen to sample the relatively narrow wet-meadow habitats surrounding wetlands. Each pair of upland and wet-meadow habitats was sampled with both mark-recapture and removal survey methods. However, removal surveys detected a greater number of species and captured more individuals of those species than mark-recapture surveys (Wiewel 2003). Removal survey data were therefore used in the following analyses. Removal surveys were conducted using single rat (18 by 8.5 cm) and mouse (10 by 4.5 cm) snap trap (McGill Metal Products Co., Marengo, IL) placed at each grid location ($n = 128$ rat traps and 128 mouse traps/habitat). Removal surveys were carried out for 4 consecutive nights, resulting in 1024 snap trap nights/habitat/WPA. Snap traps were baited with a mixture of peanut butter and oats. Snap traps were checked each morning, and captured animals were examined to determine species, sex, age, and reproductive condition. All small

mammal trapping and handling procedures followed guidelines approved by the American Society of Mammalogists (Animal Care and Use Committee 1998), the Northern Prairie Wildlife Research Center's Animal Care and Use Guidelines, and the Iowa State University Committee on Animal Care.

Characterization of Soil Moisture and Vegetation in Upland and Wet-Meadow Habitats

Analyses of soil moisture and vegetation characteristics were conducted between paired upland and wet-meadow habitats (hereafter, macrohabitat) and within each habitat (i.e., between trap locations within each habitat; hereafter, microhabitat). Because of differences in the suite of variables and sampling protocol between years, each year will be described separately. In 2001, soil moisture and vegetation characteristics were sampled systematically at 20 equally spaced points along a diagonal transect across each habitat. At each sampling point, visual obstruction measurements were taken from the 4 cardinal directions following the technique described by Robel et al. (1970). The 4 Robel measurements were recorded to the nearest half decimeter and averaged to produce a single visual obstruction value for each sampling point. The height of the standing vegetation and the depth of the litter layer at each sampling point were measured to the nearest centimeter. Percent cover, characterized as % grass + standing dead vegetation, % forb + woody vegetation, and % bare ground, was estimated within a 20 cm by 50 cm frame at each sample point. In addition, the dominant vegetation (1 to 4 species) at each sampling point was identified. Finally, the soil moisture at each sampling point was categorized as dry, damp, or saturated (scaled from 1 to 3, respectively). In 2001, all soil moisture and vegetation sampling was conducted during the week of small mammal removal surveys on each habitat.

In 2002, each habitat was divided into quarters and 5 random trap locations were selected for sampling from each quarter, resulting in 20 stratified random samples per habitat. Vegetation sampling followed the protocol utilized in 2001, with the following improvements. Percent cover was characterized as % grass vegetation, % forb vegetation, % woody vegetation, % litter, and % bare ground. Soil moisture was measured using an electronic soil moisture meter (Lincoln Irrigation, Lincoln, NE) placed 2.5 cm below the soil surface. This meter provided soil moisture readings scaled from 0 (dry) to 10 (saturated). As

in 2001, soil moisture and vegetation characteristics were sampled during the week of small mammal removal surveys. In addition, soil moisture and vegetation sampling was conducted a second time between August 5 and 8 on a new set of 20 stratified random trap locations (with the exception of 1 upland mowed prior to the second round of sampling).

Statistical Analysis

The relative abundance of small mammals was defined as the total number of unique individuals captured (M_{t+1} , Otis et al. 1978) during removal surveys in each habitat. M_{t+1} is proportional to population size, although proportionality likely varies among species (Slade and Blair 2000) and perhaps across space and time. However, limited captures of species other than meadow voles precluded the estimation of abundance for other species, necessitating the use of an index of relative abundance. Species richness (S), evenness (E), and diversity (H') were calculated for each sampled habitat following the methods described by Hayek and Buzas (1997:379).

Differences in mean small mammal relative abundance and diversity between upland and wet-meadow habitats were tested using unpaired t-test analyses in 2001 and paired t-test analysis in 2002 (Proc TTEST, SAS Institute 1999), when habitats were paired on each WPA. Differences between upland and wet-meadow soil moisture and vegetation characteristics were investigated using generalized linear models (Proc MIXED, SAS Institute 1999). Preliminary analyses indicated that, with the exception of soil moisture, variation of vegetation characteristics was much greater among WPAs than between paired habitats within WPAs. Because the primary focus of vegetation analysis was to differentiate between upland and wet-meadow habitats, rather than between WPAs, habitat was treated as a fixed effect and WPA and the WPA*habitat interaction were treated as random effects during all analyses. Each year was analyzed separately because of the differences in soil moisture and vegetation sampling protocols described previously.

Associations between the relative abundance, diversity, and distribution of small mammals and soil moisture and vegetation characteristics were investigated using Spearman rank-order correlation (r_s) analysis (Sokal and Rohlf 1995; Proc CORR, SAS Institute 1999). Correlations were computed at both the macrohabitat and microhabitat levels. Macrohabitat

analyses were based on pooled soil moisture and vegetation characteristics from the 20 sampled points on each upland and wet-meadow habitat. At this scale, species may respond differently to soil moisture and vegetation characteristics. For example, the abundance of a habitat specialist species might be associated with some threshold level of a specific vegetative characteristic, whereas the abundance of a generalist species might be better explained by the variability of vegetative characteristics. Thus, macrohabitat analyses included both median values and the relative variability, measured by the coefficient of variation (CV, Sokal and Rohlf 1995), of soil moisture and vegetation characteristics. Medians were chosen instead of means because many of the sampled vegetation characteristics were highly skewed and contained multiple zero values; medians represented “typical” values and better approximated a normal distribution. Microhabitat analyses were based on soil moisture and vegetation characteristics of individual sampled trap locations within upland and wet-meadow habitats. In addition to soil moisture and vegetation characteristics, a dummy habitat variable (coded 0 for upland habitats and 1 for wet-meadow habitats) was included in all microhabitat analyses. In all macrohabitat and microhabitat correlation analyses, coefficients of determination ($r_s^2 \geq |0.50|$) were interpreted as having biological significance (P. M. Dixon, Iowa State University Dept. of Statistics, personal communication).

In addition to standard correlation analyses, spatial patterns in small mammal distribution at the microhabitat level were investigated using spatial autocorrelation and cross-correlation analyses (Rossi et al. 1992, Burrough 1995). Spatial autocorrelation analysis was used to test whether the likelihood of capturing a species at a specific trap was positively or negatively associated with the presence of the same species in nearby traps (Burrough 1995). The modeled response was the number of captures of a small mammal species at each trap location. Spatial autocorrelation ($\hat{r}(h)$) was calculated for each small mammal species, on each sampled habitat, as:

$$\hat{r}(h) = \frac{\frac{1}{N(h)} \sum_{i=1}^{N(h)} [(x_{(i)} - \bar{x})(x_{(i+h)} - \bar{x})]}{\sigma^2},$$

where h is the lag distance, $N(h)$ is the total number of pairs of trap locations separated by lag distance h , $x_{(i)}$ and $x_{(i+h)}$ are the number of captures at two data points separated by lag distance h , and σ^2 is the variance in the response variable (Rossi et al. 1992). The significance of $\hat{r}(h)$ values were assessed by comparison with 95% confidence limits, calculated as $\frac{-1}{N} \pm \frac{2}{\sqrt{N}}$ (K. A. Moloney, personal communication); $\hat{r}(h)$ values greater than the upper confidence limit were interpreted as positive autocorrelation, whereas values less than the lower confidence limit were interpreted as negative autocorrelation. Results of spatial autocorrelation analyses were summarized for each species by calculating mean $\hat{r}(h)$ values at each lag distance h and comparing with mean 95% confidence limits.

Spatial cross-correlation analysis was used to test whether spatial patterns in soil moisture and vegetation characteristics were associated with the distribution of small mammals at the microhabitat level. The modeled response variables were the various soil moisture and vegetation characteristics and the number of captures of a small mammal species at each trap location. Spatial cross-correlation ($\hat{r}_{xy}(h)$) was calculated for soil moisture and vegetation characteristics on each sampled habitat as:

$$\hat{r}_{xy}(h) = \frac{\frac{1}{N(h)} \sum_{i=1}^{N(h)} [(x_{(i)} - \bar{x})(y_{(i+h)} - \bar{y})]}{\sqrt{\sigma_x^2 \sigma_y^2}},$$

where x represents the number of captures of a small mammal species at a trap location and y represents the vegetation or soil moisture response variable (Rossi et al. 1992). The significance of $\hat{r}_{xy}(h)$ values were assessed by comparison with 95% confidence limits,

calculated as $0 \pm \frac{2}{\sqrt{N}}$ (K. A. Moloney, personal communication), and interpreted in the same fashion as described for spatial autocorrelation. Results of spatial cross-correlation analyses were summarized for each soil moisture and vegetation characteristic by calculating mean $\hat{r}_{xy}(h)$ values at each lag distance h and comparing with mean 95% confidence limits.

Because soil moisture and vegetation characteristics were sampled at only 20 trap locations per habitat, spatial cross-correlation analyses were limited to meadow voles, the only species captured commonly enough for adequate sample sizes.

Soil moisture and vegetation characteristics identified in correlation analyses were used to develop predictive models of the abundance and diversity of small mammals at the macrohabitat level, and of the distribution of small mammals at the microhabitat level.

Predictive models of the relative abundance and diversity of small mammals as a function of macrohabitat-level soil moisture and vegetation characteristics were developed using multiple stepwise regression (Proc REG, SAS Institute 1999). Predictive models of the presence of small mammals at specific trap locations as a function of microhabitat-level soil moisture and vegetation characteristics were developed using stepwise logistic regression (Proc LOGISTIC, SAS Institute 1999). The latter models had the general form:

$$\text{logit}(p_i) = \log\left(\frac{p_i}{1-p_i}\right) = f(\text{microhabitat-level vegetation and soil moisture characteristics}),$$

where the dependent variable, p_i , was the presence of at least 1 small mammal in a trap during the 4-night removal survey. Only trap locations where soil moisture and vegetation characteristics were sampled could be included in microhabitat-level models, which restricted microhabitat analyses to upland and wet-meadow habitats surveyed in 2002, and perhaps limited the resolution of this analysis. Soil moisture and vegetation characteristics with bivariate correlations (r_s) $\geq |0.80|$ were not allowed to co-enter predictive models (P. M. Dixon, Iowa State University Dept. of Statistics, personal communication). In this situation, only the variable with the higher correlation with the response variable was allowed to enter into regression analyses. In addition, variance inflation factors (Proc REG, SAS Institute 1999:2967; Miles and Shevlin 2001:130) were examined to prevent highly correlated combinations of independent variables from entering predictive models. The goodness of fit of predictive models selected by regression procedures was assessed based on the coefficient of determination (r^2) and, in the case of microhabitat-level logistic models, the Hosmer-Lemeshow statistic (χ^2_{HL} , Hosmer and Lemeshow 1989:140-145).

RESULTS

Small Mammal Community

A total of 3,758 unique individuals of 10 species were captured during 34,816 trap nights of small mammal removal surveys in 2001 and 2002 (Table 1). The small mammal

community was dominated by the meadow vole, which made up 76.7% of total captures and was the most frequently captured species in both upland and wet-meadow habitats in 2001 and 2002 (Table 1). Thirteen-lined ground squirrels, meadow jumping mice, masked shrews (*Sorex cinereus*), deer mice, and Franklin's ground squirrels made up 1.6–6.8% of total captures (Table 1). Northern short-tailed shrews (*Blarina brevicauda*), Northern pocket gophers (*Thomomys talpoides*), least weasels (*Mustela nivalis*), and house mice (*Mus musculus*) were captured infrequently (Table 1) and were excluded from all analyses except those involving S, E, and H'.

In 2001, there were no significant differences in the total number of small mammals captured (mean difference = 12.1, $t = 0.37$, $df = 10$, $P = 0.718$) or the number of captures of individual species (mean differences = 0–8.9, $t = 0–1.07$, $df = 10$, $P = 0.242–1.0$) between upland and wet-meadow habitats (Table 1). In 2002, more total small mammals were captured in wet-meadow habitats than in upland habitats (mean difference = 35.3, paired $t = 3.14$, $df = 10$, $P = 0.011$). In addition, the relative abundance of meadow voles was significantly greater in wet-meadow habitats (mean difference = 36.4, paired $t = 2.81$, $df = 10$, $P = 0.018$), whereas the relative abundance of masked shrews was significantly greater in upland habitats (mean difference = 3.6, paired $t = 2.86$, $df = 10$, $P = 0.017$) (Table 1). There was weak evidence that thirteen-lined ground squirrels were more abundant in upland habitats (mean difference = 4.1, paired $t = 1.92$, $df = 10$, $P = 0.083$) and that meadow jumping mice were more abundant in wet-meadow habitats (mean difference = 7.6, paired $t = 1.93$, $df = 10$, $P = 0.083$). There was no significant difference in the number of deer mice (mean difference = 1.36, paired $t = 0.62$, $df = 10$, $P = 0.547$) or Franklin's ground squirrels (mean difference = 0.18, paired $t = 0.17$, $df = 10$, $P = 0.869$) captured in upland and wet-meadow habitats (Table 1). There were only slight differences in mean small mammal species richness, evenness, and diversity between upland and wet-meadow habitats in 2001 and 2002 (Table 2), and none of these differences were significant (Table 2).

Soil Moisture and Vegetation Characteristics of Upland and Wet-Meadow Habitats

In 2001, none of the sampled soil moisture or vegetation characteristics differed significantly between upland and wet-meadow habitats ($F = 0–3.11$, $df = 1, 3$, $P = 0.176–$

0.968) after controlling for between-WPA variation (Table 3). In 2002, during the first vegetation sampling period coinciding with small mammal removal surveys (Table 4), wet-meadow habitats had significantly higher mean soil moisture ($F = 41.27$, $df = 1, 10$, $P < 0.001$) than upland habitats and there was weak evidence that mean Robel visual obstruction was greater in wet-meadow habitats ($F = 4.88$, $df = 1, 10$, $P = 0.052$), after controlling for between-WPA variation. Differences between upland and wet-meadow habitats were more apparent during the second vegetation sampling period in early August (Table 4). Mean Robel visual obstruction ($F = 17.07$, $df = 1, 9$, $P = 0.003$), vegetation height ($F = 11.63$, $df = 1, 9$, $P = 0.008$), soil moisture ($F = 85.56$, $df = 1, 9$, $p < 0.001$), and % forb vegetation ($F = 31.38$, $df = 1, 9$, $P < 0.001$) were greater in wet-meadow habitats after controlling for between-WPA variation (Table 4). In contrast, upland habitats had greater mean % litter ($F = 9.77$, $df = 1, 9$, $P = 0.012$) than wet-meadow habitats after controlling for between-WPA variation (Table 4).

Small Mammal–Macrohabitat Associations

Correlation analyses revealed general patterns of association between the relative abundance and diversity of small mammals and macrohabitat-level soil moisture and vegetation characteristics (Tables 5, 6, 7). In 2001, median Robel visual obstruction, the relative variability (CV) of soil moisture, the relative variability (CV) of % bare ground, and median litter depth were each correlated with the relative abundance of several species and with species richness (Table 5). More specifically, the relative abundance of meadow voles, and the total relative abundance of small mammals, was positively correlated with median % forb + woody vegetation and negatively correlated with median % grass + standing dead vegetation, the relative variability (CV) of % forb + woody vegetation, and median % bare ground (Table 5). Species richness and the relative abundance of deer mice and Franklin's ground squirrels were positively correlated with median Robel visual obstruction, the relative variability (CV) of soil moisture, and the relative variability (CV) of % bare ground, and negatively correlated with median litter depth (Table 5). Evenness was positively correlated with median % grass + standing dead vegetation and the relative variability (CV) of % forb + woody vegetation, and negatively correlated with median % forb + woody vegetation (Table

5). Diversity was positively correlated with the relative variability (CV) of soil moisture and negatively correlated with median litter depth (Table 5).

In 2002, median soil moisture measured during removal surveys was positively correlated with the relative abundance of meadow voles and negatively correlated with the relative abundance of deer mice, whereas the relative variability (CV) of soil moisture was negatively correlated with meadow vole abundance and positively correlated with deer mouse abundance (Table 6). The relative abundance of thirteen-lined ground squirrels was positively correlated with median % forb vegetation and negatively correlated with median % litter measured during removal surveys (Table 6). Both evenness and diversity were negatively correlated with median soil moisture measured during removal surveys (Table 6). In general, soil moisture and vegetation characteristics sampled in early August were not strongly correlated with small mammal abundance or diversity (Table 7), although median soil moisture was positively correlated with meadow vole and total small mammal relative abundance and median litter depth was negatively correlated with the relative abundance of masked shrews (Table 7).

Small Mammal–Microhabitat Associations

At the microhabitat level, there were few strong correlations between soil moisture or vegetation characteristics and the distribution of small mammals in 2002 (Table 8, 9). One exception was litter depth at the time of removal surveys, which was negatively correlated with the presence of masked shrews at specific trap locations (Table 8). Soil moisture and vegetation characteristics sampled in early August were not strongly correlated with the distribution of small mammals at the microhabitat level (Table 9).

There was little evidence of species-specific spatial autocorrelation in the presence of small mammals at individual trap locations, with the exception of a slight positive autocorrelation for meadow voles at lag distances of 10 and 20 m (Figure 1A) and meadow jumping mice at a lag distance of 10 m (Figure 1B). Cross-correlation analyses revealed no significant associations between the spatial distribution of meadow voles and the spatial patterns in soil moisture and vegetation characteristics sampled at individual trap locations (Figure 2).

Predictive Models

Macrohabitat-level Predictive Models.—In general, soil moisture and vegetation characteristics associated with small mammal abundance and diversity were also important components of macrohabitat-level predictive models. There were no instances in predictive models in which variance inflation factors suggested problematic collinearity between independent variables. In 2001, predictive models of small mammal relative abundance and diversity generally contained one or more of the following variables: the relative variability (CV) of % forb + woody vegetation, the relative variability (CV) of soil moisture, and median litter depth, although none of the sampled soil moisture or vegetation characteristics made significant contributions to a predictive model of the relative abundance of meadow jumping mice at the macrohabitat level (Table 10). Predictive models explained 36.8–94.7% of the variation in the relative abundance and diversity of small mammals at the macrohabitat level (Table 10). For example, the best predictive model of the relative abundance of meadow voles included the relative variability (CV) of % forb + woody vegetation and explained 60.2% of the variation in meadow vole relative abundance at the macrohabitat level (Table 10). The best predictive model of Franklin’s ground squirrel relative abundance included the median and relative variability (CV) of soil moisture and the median and relative variability (CV) of litter depth and explained 94.7% of the variation in Franklin’s ground squirrel relative abundance at the macrohabitat level (Table 10). Predictive models of both deer mouse relative abundance and species richness included median soil moisture and median litter depth (Table 10). These models explained 76.3% and 70.7% of the variation in the relative abundance of deer mice and species richness, respectively, at the macrohabitat level (Table 10). The best predictive model of diversity included median litter depth and explained 46.4% of the variation in diversity at the macrohabitat level (Table 10).

In 2002, predictive models generated from macrohabitat-level soil moisture and vegetation characteristics sampled during small mammal removal surveys included a more diverse mix of soil moisture and vegetation characteristics than equivalent models from 2001. Nonetheless, the most common soil moisture and vegetation characteristics in predictive models were similar and included median soil moisture, the relative variability (CV) of soil

moisture, median % forb vegetation, and the relative variability (CV) of % litter (Table 11). In general, 2002 models explained similar or slightly lower amounts of variation in small mammal relative abundance and diversity (24.8–75.6%) than equivalent 2001 models, with the exception of models predicting the relative abundance of masked shrews and diversity at the macrohabitat level (Table 11). The best predictive model of the relative abundance of meadow voles included median soil moisture and explained 27.8% of the variation in meadow vole relative abundance at the macrohabitat level (Table 11). Predictive models of the relative abundance of masked shrews, total small mammal relative abundance, and species richness at the macrohabitat level included median soil moisture and median % forb vegetation (Table 11). These models explained 74.3%, 36.4%, and 45.7% of the variation in masked shrew relative abundance, total small mammal relative abundance, and species richness, respectively (Table 11). The best predictive model of small mammal diversity included median Robel visual obstruction, the relative variability (CV) of soil moisture, median % woody vegetation, and the relative variability (CV) of % litter and explained 75.6% of the variation in diversity at the macrohabitat level (Table 11).

Predictive models generated from macrohabitat-level soil moisture and vegetation characteristics sampled in early August, 2002, generally explained less variation in small mammal relative abundance and diversity (19.2–50.5%) than equivalent models based upon soil moisture and vegetation characteristics sampled concurrently with small mammal surveys, with the exception of meadow vole relative abundance and evenness (Table 12). Again, predictive models commonly included median soil moisture and median % bare ground was also important in several predictive models (Table 12). However, none of the sampled soil moisture or vegetation characteristics made significant contributions to predictive models of the relative abundance of masked shrews, deer mice, or Franklin's ground squirrels at the macrohabitat level (Table 12). The best predictive model of the relative abundance of meadow voles included only median soil moisture and explained 38.8% of the variation in meadow vole abundance at the macrohabitat level (Table 12). Predictive models of both evenness and diversity included median soil moisture and the relative variability (CV) of % bare ground (Table 12). These models explained 50.5% and

40.1% of the variation in evenness and diversity, respectively, at the macrohabitat level (Table 12).

Microhabitat-level Predictive Models.—Predictive models were also generated from microhabitat-level soil moisture and vegetation characteristics sampled at specific trap locations in 2002. In general, these models included a broad array of soil moisture and vegetation characteristics, although the most common variable in predictive models was again soil moisture (Table 13, 14). None of the soil moisture or vegetation characteristics made significant contributions to predictive models of the presence of thirteen-lined ground squirrels (Table 13, 14), masked shrews (Table 14), or deer mice (Table 14) at specific trap locations. Predictive models generated from microhabitat-level soil moisture and vegetation characteristics sampled during removal surveys explained 5.0–15.3% of the variation in the presence of small mammals at a trap location (Table 13). The best predictive model of the presence of meadow voles at a trap location included soil moisture and litter depth, but explained only 7.3% of the variation in the presence of meadow voles at specific trap locations (Table 13). The best predictive model of the presence of masked shrews at a trap location included habitat, vegetation height, and % forb vegetation and explained 15.3% of the variation in the presence of masked shrews at specific trap locations (Table 13). The best predictive model of the presence of any small mammal species at a specific trap location included vegetation height, soil moisture, and % forb vegetation and explained 9.1% of the variation in the presence of any small mammal at a trap location (Table 13).

Microhabitat-level predictive models generated from soil moisture and vegetation characteristics sampled in early August generally explained more variation (7.5–53.8%) in the presence of small mammals at specific trap locations than equivalent models generated from soil moisture and vegetation characteristics sampled during removal surveys (Table 14). The best predictive model of the presence of meadow voles at a trap location included soil moisture and % woody vegetation and explained 14.2% of the variation in the presence of meadow voles at specific trap locations (Table 14). The best predictive model of the presence of Franklin's ground squirrels at a trap location included habitat, soil moisture, and % grass vegetation and explained 53.8% of the variation in the presence of Franklin's ground

squirrels at specific trap locations (Table 14). The best predictive model of the presence of any small mammal species at a specific trap location included only soil moisture and explained 9.5% of the variation in the presence of any small mammal at a trap location (Table 14).

DISCUSSION

Small Mammal Community

Meadow voles were the most common species in both upland and wet-meadow habitats in 2001 and 2002. All common species of small mammals were found in both habitats; however, masked shrews and thirteen-lined ground squirrels were generally more abundant in upland habitats, whereas meadow voles and meadow jumping mice were generally more abundant in wet-meadow habitats. Deer mice were equally abundant in both habitats, as expected based on their generalist life history (Grant et al. 1977, Abramsky et al. 1979, Snyder and Best 1988, Clark et al. 1989). Differences in species richness, evenness, and diversity between upland and wet-meadow habitats were nonsignificant, most likely because of the similarity in soil moisture and vegetation characteristics between the two habitats which may have minimized the effect of any true habitat preferences by small mammals.

Soil Moisture and Vegetation Characteristics of Upland and Wet-Meadow Habitats

Soil moisture and vegetation characteristics sampled in upland and wet-meadow habitats did not differ as much as expected based on a priori selection of paired habitats. In part, the lack of significant differences between soil moisture and vegetation characteristics of upland and wet-meadow habitats may be attributed to the highly variable weather patterns of the Northern Great Plains. In 2001, when upland and wet-meadow habitats were very similar, spring and summer rainfall totals in western Stutsman County were approximately 125-150% of 30-year average (North Dakota Agricultural Weather Network 2003). In contrast, upland and wet-meadow habitats were less similar in 2002, when spring and summer rainfall totals were 80-100% of 30-year average (North Dakota Agricultural Weather Network 2003). In addition, the effects of previous land use and management history have had a strong influence on differences between WPAs, and even differences between different areas within WPAs. WPAs are often former pasture or hay land with habitats dominated by a few vegetative

species such as smooth brome (*Bromus inermis*), Kentucky bluegrass (*Poa pratensis*), and alfalfa (*Medicago sativa*). Often, management practices act to further homogenize grassland habitats on WPAs. Thus, differences between WPAs are often much greater than differences between upland and wet-meadow habitats within WPAs.

Small Mammal–Macrohabitat Associations

Despite the variability in soil moisture and vegetation characteristics of upland and wet-meadow habitats, these analyses suggest that small mammals are responding to gradients in soil moisture and vegetation characteristics at the macrohabitat level. For example, meadow voles were most abundant in areas with high soil moisture and % forb vegetation and low % bare ground, which is consistent with many accounts of the habitat preferences of this species (Getz 1961a, 1970, 1971; Birney et al. 1976; Snyder and Best 1988). Thirteen-lined ground squirrels were most abundant in areas with low % litter, as expected based on their known preference for relatively open areas (Grant et al. 1977, Abramsky et al. 1979, Clark et al. 1989). Meadow jumping mice, deer mice, and Franklin's ground squirrels were most common in heterogenous areas with a mixture of dense vegetation and bare ground and low litter depths (Getz 1961c, Grant et al. 1977, Abramsky et al. 1979, Kaufman et al. 1988, Snyder and Best 1988, Clark et al. 1989).

Small Mammal–Microhabitat Associations

Correlation and spatial autocorrelation and cross-correlation analyses revealed few strong associations between microhabitat soil moisture or vegetation characteristics and the distribution of small mammals within upland and wet-meadow habitats. Numerous researchers have found similar results (Morris 1987, Jorgensen and Demarais 1999). Jorgensen and Demarais (1999) suggest that if suitable microhabitat conditions are available in all macrohabitats, it is unlikely that small mammal relative abundance and diversity will be strongly associated with microhabitat conditions. Instead, relative abundance and diversity are determined at the macrohabitat level (Morris 1987, Jorgensen and Demarais 1999). This phenomenon may be even stronger in WPAs, where management practices may make macrohabitats and microhabitats more similar. Alternatively, because microhabitat analyses were limited to the 20 trap locations per habitat where soil moisture and vegetation

characteristics were sampled, it is possible that microhabitat associations may have gone undetected because of sample size limitations.

Predictive Models

Predictive models based on macrohabitat-level soil moisture and vegetation characteristics generally explained moderate amounts of the variation in small mammal abundance and diversity, but did not always agree between years. These year-to-year differences were likely the result of weather differences and soil moisture and vegetation sampling protocol differences. Important macrohabitat-level soil moisture and vegetation characteristics in both 2001 and 2002 included median soil moisture, the relative variability (CV) of soil moisture, and median litter depth. Other soil moisture and vegetation characteristics included in predictive models for several species of small mammals in a single year included the relative variability (CV) of % forb + woody vegetation in 2001 and median % forb vegetation, the relative variability (CV) of % litter, and the relative variability (CV) of % bare ground in 2002. In general, predictive models followed a few common patterns. The relative abundance of meadow voles was predicted to increase as the relative variability (CV) of % forb + woody vegetation decreased (Table 10), and as soil moisture increased (Table 11, 12). These results agree with previous accounts of the habitat preferences of meadow voles in grassland habitats (Getz 1961a, 1970, 1971; Birney et al. 1976; Snyder and Best 1988). The relative abundance of thirteen-lined ground squirrels was predicted to decrease as litter depth increased (Table 10, 11, 12), supporting documented preference of this species for open habitats with patches of bare ground (Grant et al. 1977, Abramsky et al. 1979, Clark et al. 1989). The relative abundance of masked shrews and Franklin's ground squirrels were predicted to increase as % forb vegetation increased (Table 11), supporting the notion that these species favor areas of dense vegetation (Getz 1961b, Erlie and Tester 1984).

In 2002, species richness and evenness were predicted to increase as soil moisture decreased, and diversity was predicted to increase as the relative variability in soil moisture increased (Table 11). These results suggest that species richness, evenness, and diversity should be greater in upland habitats, which generally had lower soil moisture and less variability in soil moisture than wet-meadow habitats (Table 4). Although species richness,

evenness, and diversity were not significantly different between upland and wet-meadow habitats (Table 2), each was greater, on average, in upland habitats.

Predictive models based on microhabitat-level soil moisture and vegetation characteristics generally explained low amounts of the variation of the presence of small mammals at specific trap locations. Nonetheless, these predictive models still offer some insight into microhabitat preferences of small mammals. At the microhabitat level, the likelihood of meadow voles being present at a specific trap location was predicted to increase as soil moisture and litter depth increased, which agrees with previous research of microhabitat preferences of this species (Getz 1961a, 1970, 1971; Birney et al. 1976; Snyder and Best 1988). The likelihood of the presence of meadow jumping mice at a trap location was predicted to increase as the density of vegetation and the amount of woody vegetation increased, agreeing with other accounts of microhabitat preferences of this species (Getz 1961c). The presence of deer mice at a trap location was also predicted to increase as vegetation density increased, although this result is contrary to many accounts of the microhabitat preferences of deer mice (Grant et al. 1977, Abramsky et al. 1979, Clark et al. 1989).

The ultimate goal of these macrohabitat and microhabitat models was to predict the relative abundance, diversity, and distribution of small mammal populations in upland and wet-meadow habitats. Predictive models generally explained a moderate proportion of the variation in small mammal relative abundance and diversity at the macrohabitat level, but often explained only low proportions of the variation in small mammal distribution at the microhabitat level. Notably, predictive models explained only about 30% of the variation in meadow vole abundance at the macrohabitat level in 2002 (Table 11, 12). Because meadow voles were by far the most common species in both upland and wet-meadow habitats, predicting their abundance is essential to predicting available small mammal prey.

Nonetheless, soil moisture and vegetation characteristics identified as being associated with small mammal relative abundance, diversity, and distribution during correlation and regression analyses usually agreed with published accounts of small mammal macrohabitat and microhabitat preferences. This suggests that the observed relationships were biologically

meaningful and that further study of small mammal–habitat associations in upland and wet-meadow grassland habitats is warranted. One interesting possibility involves the use of remotely-sensed data. Many of the soil moisture and vegetation characteristics identified as being associated with small mammal relative abundance, diversity, and distribution in this study, especially soil moisture and % cover of different vegetation types, can be identified using remotely-sensed data. For example, remotely-sensed data have been used to identify and classify wet-meadow habitats (Kindscher et al. 1998) and to differentiate between different vegetation types (e.g., grass vs. shrub) (Duncan et al. 1993, Hope et al. 1993, Jakubauskas et al. 2001). The use of remotely-sensed data to assess soil moisture and vegetation characteristics could allow researchers to predict small mammal prey abundance and diversity at much larger scales than currently possible. Although remotely-sensed data are often less precise than ground-based sampling (Hope et al. 1993), the benefits gained from sampling across large areas would likely counterbalance the loss of precision.

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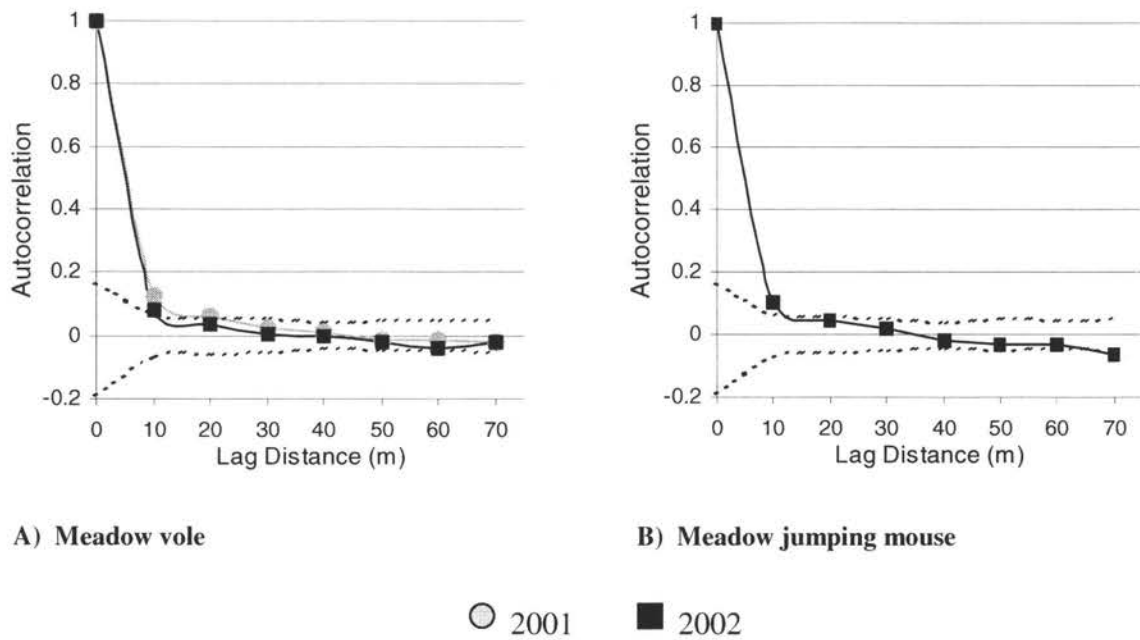
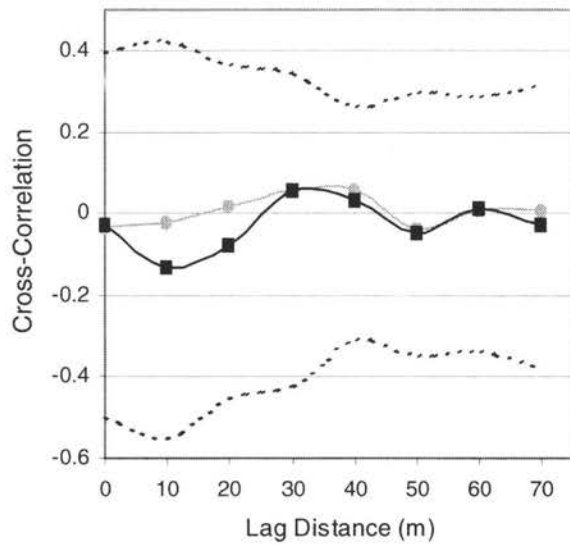
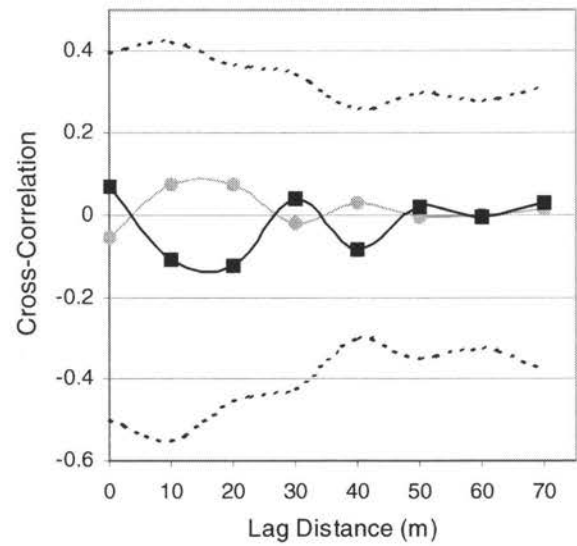


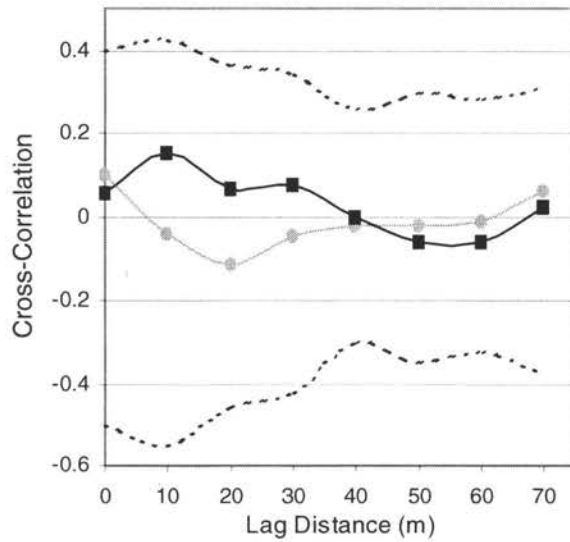
Figure 1. Spatial autocorrelation ($\hat{f}(h)$) in the distribution of meadow voles (A) and meadow jumping mice (2002 only; B) captured during small mammal removal surveys in upland and wet-meadow habitats on Waterfowl Production Areas in Stutsman County, ND, 2001-2002. Solid lines indicate mean $\hat{f}(h)$ values for 2001-2002. Broken lines indicate 95 % confidence intervals.



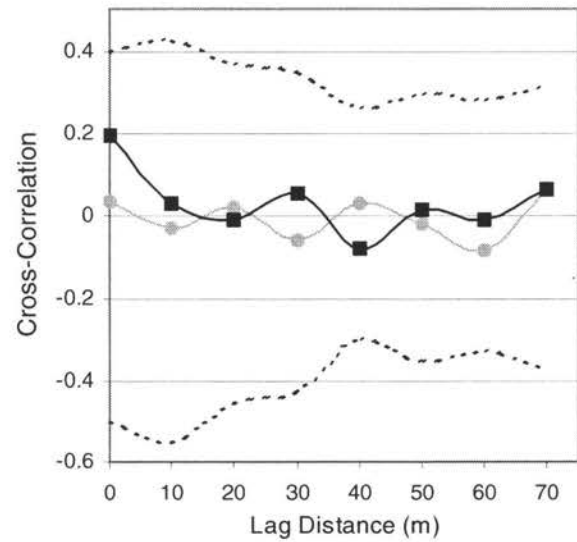
A) Robel Visual Obstruction



B) Soil Moisture



C) % Forb Vegetation



D) Litter Depth

○ Upland Habitats

■ Wet Meadow Habitats

Figure 2. Cross-correlation ($\hat{r}_{xy}(h)$) between the spatial distribution of meadow voles and Robel visual obstruction (A), soil moisture (B), % forb vegetation (C), and litter depth (D) sampled in upland and wet-meadow habitats on Waterfowl Production Areas in Stutsman County, ND, 2001-2002. Solid lines indicate mean $\hat{r}_{xy}(h)$ values at lag h for upland and wet-meadow habitats in 2001-2002. Broken lines indicate 95 % confidence intervals.

Table 1. Total and mean number of unique individuals captured (M_{t+1}) during 4-day removal surveys on 1.05 ha, 256-trap grids in upland and wet-meadow habitats on Waterfowl Production Areas in Stutsman County, ND, 2001-2002. Number of sampled locations (n) indicated for each year and habitat.

Species	2001						2002						Years and Habitats Combined		
	Upland n = 8			Wet Meadow n = 4			Upland n = 11			Wet Meadow n = 11					
	Total M_{t+1}	\overline{M}_{t+1}	SE	Total M_{t+1}	\overline{M}_{t+1}	SE	Total M_{t+1}	\overline{M}_{t+1}	SE	Total M_{t+1}	\overline{M}_{t+1}	SE	Total M_{t+1}	\overline{M}_{t+1}	SE
Meadow vole (<i>Microtus pennsylvanicus</i>)	829	103.63	15.57	379	94.75	30.96	638	58.00	15.75	1,038	94.36	20.16	2,884	84.82	9.87
Thirteen-lined ground squirrel (<i>Spermophilus tridecemlineatus</i>)	52	6.50	2.24	26	6.50	3.66	112	10.18	2.32	67	6.09	1.50	257	7.56	1.12
Meadow jumping mouse (<i>Zapus hudsonius</i>)	26	3.25	0.56	18	4.50	1.94	57	5.18	1.41	141	12.82	4.28	242	7.12	1.59
Masked shrew (<i>Sorex cinereus</i>)	11	1.38	0.57	8	2.00	0.41	87	7.91	2.83	48	4.36	2.32	154	4.53	1.24
Deer mouse (<i>Peromyscus maniculatus</i>)	36	4.50	1.58	7	1.75	1.75	56	5.09	1.68	41	3.73	1.29	140	4.12	0.79
Franklin's ground squirrel (<i>Spermophilus franklinii</i>)	27	3.38	1.41	3	0.75	0.75	15	1.36	0.73	17	1.55	1.06	62	1.82	0.54
Northern short-tailed shrew (<i>Blarina brevicauda</i>)	2	0.25	0.16				3	0.27	0.27	2	0.18	0.18	7	0.21	0.11
Northern pocket gopher (<i>Thomomys talpoides</i>)				1	0.25	0.25	3	0.27	0.20	2	0.18	0.12	6	0.18	0.08
Least weasel (<i>Mustela nivalis</i>)				1	0.25	0.25	2	0.18	0.12	1	0.09	0.09	4	0.12	0.06
House mouse (<i>Mus musculus</i>)										2	0.18	0.18	2	0.06	0.06
Unidentifiable Species	7	0.88	3.98	4	1.00	0.58	3	0.27	0.14	15	1.36	0.51	29	0.85	0.21
Total Captures ^a	983	122.88	18.36	443	110.75	28.21	973	88.45	17.10	1,359	123.55	20.00	3,758	110.53	10.04

^a Excluding Unidentifiable Species.

Table 2. Total and mean (\bar{X}) small mammal species richness (S), mean evenness (E), and mean diversity (H'), calculated using all species captured during 4-day removal surveys on 1.05 ha, 256-trap grids in upland and wet-meadow habitats on Waterfowl Production Areas in Stutsman County, ND, 2001-2002. S, E, and H' calculated following the methods detailed in Hayek and Buzas (1997:379). Number of sampled locations (n) indicated for each year and habitat.

	2001								2002							
	Upland n = 8				Wet Meadow n = 4				Upland n = 11				Wet Meadow n = 11			
	Total	\bar{X}	SE	Total	\bar{X}	SE	t ^a	P	Total	\bar{X}	SE	Total	\bar{X}	SE	t ^b	P
S	7	5.0	0.57	8	5.0	1.00	0.00	1.000	9	5.4	0.49	10	4.6	0.45	1.39	0.195
E		0.4	0.02		0.4	0.05	0.69	0.506		0.6	0.04		0.5	0.04	1.37	0.202
H'		0.6	0.11		0.7	0.24	0.26	0.798		1.0	0.12		0.8	0.14	1.67	0.125

^a Unpaired t-test, df = 10

^b Paired t-test, df = 10

Table 3. Mean (\bar{X}) soil moisture and vegetation characteristics sampled at 20 systematic points in 8 upland and 4 wet-meadow habitats on Waterfowl Production Areas in Stutsman County, ND, in 2001. Total number (n) of soil moisture and vegetation characteristic sampling points indicated for each habitat.

	Upland n = 160		Wet Meadow n = 80		F ^a	P
	\bar{X}	SE	\bar{X}	SE		
Robel Visual Obstruction (dm)	4.19	0.09	3.60	0.14	0.00	0.968
Vegetation Height (cm)	65.80	1.43	58.59	1.79	3.11	0.176
Soil Moisture ^b	2.09	0.03	2.18	0.04	0.81	0.434
% Grass + Standing Dead Vegetation	72.68	2.19	74.75	2.52	0.04	0.855
% Forb + Woody Vegetation	26.89	2.20	24.89	2.55	0.03	0.875
% Bare Ground	0.43	0.12	0.36	0.09	2.01	0.251
Litter Depth (cm)	6.44	0.27	8.64	0.34	0.54	0.517

^a df = 1, 3

^b Soil moisture measurements scaled from 1 (dry) to 3 (saturated).

Table 4. Mean (\bar{X}) soil moisture and vegetation characteristics sampled at 20 stratified random points in 11 upland and 11 wet-meadow habitats on Waterfowl Production Areas in Stutsman County, ND, in 2002. Soil moisture and vegetation characteristic sampling occurred concurrently with small mammal removal surveys and August 5-8. Total number (n) of sampling points indicated for each habitat.

	Removal Survey Week						August 5-8					
	Upland n = 220		Wet Meadow n = 220		F ^a	P	Upland n = 200		Wet Meadow n = 220		F ^b	P
	\bar{X}	SE	\bar{X}	SE			\bar{X}	SE	\bar{X}	SE		
Robel Visual Obstruction (dm)	2.66	0.10	3.36	0.16	4.88	0.053	2.98	0.08	4.13	0.16	17.07	0.003
Vegetation Height (cm)	33.98	1.10	37.36	1.80	0.98	0.345	39.95	1.13	51.96	1.69	11.63	0.008
Soil Moisture ^c	1.36	0.10	5.70	0.23	41.27	< 0.001	3.35	0.16	7.29	0.21	85.56	< 0.001
% Grass Vegetation	24.41	1.16	24.27	1.49	0.00	0.978	28.38	1.04	31.46	1.52	0.60	0.457
% Forb Vegetation	9.71	1.13	11.55	1.29	1.07	0.326	12.13	1.02	24.32	1.44	31.38	< 0.001
% Woody Vegetation	5.05	0.97	3.14	0.76	1.50	0.250	6.00	1.01	3.18	0.74	2.28	0.168
% Litter	59.11	1.47	59.80	1.89	0.02	0.882	52.83	1.29	39.61	1.50	9.77	0.012
% Bare Ground	1.73	0.53	1.25	0.48	0.28	0.611	0.68	0.30	1.43	0.60	0.76	0.407
Litter Depth (cm)	8.29	0.20	8.93	0.24	1.16	0.307	5.39	0.23	5.82	0.25	0.87	0.374

^a df = 1, 10

^b df = 1, 9

^c Soil moisture measured using an electronic soil moisture meter (Lincoln Irrigation, Lincoln, NE) placed 2.5 cm below the soil surface. Measurements scaled from 0 (dry) to 10 (saturated).

Table 5. Spearman correlation coefficients (r_s) between the relative abundance (M_{t+1}) of small mammal species, species richness (S), evenness (E), and diversity (H') and macrohabitat-level soil moisture and vegetation characteristics sampled concurrently with small mammal surveys at 20 systematic points in upland ($n = 8$) and wet-meadow ($n = 4$) habitats on Waterfowl Production Areas in Stutsman County, ND, in 2001. The probability of each observed bivariate correlation is indicated below the correlation coefficient. Biologically significant correlations ($r_s \geq |0.50|$) are indicated in bold.

	Habitat	Robel Visual Obstruction		Vegetation Height		Soil Moisture		% Grass + Standing Dead Vegetation		% Forb + Woody Vegetation		% Bare Ground		Litter Depth	
		Median	CV	Median	CV	Median	CV	Median	CV	Median	CV	Median	CV	Median	CV
Meadow vole M_{t+1}	-0.051 0.874	0.420 0.174	-0.343 0.275	0.121 0.707	-0.007 0.983	-0.162 0.615	0.092 0.776	-0.719 0.008	-0.210 0.512	0.759 0.004	-0.795 0.002	-0.519 0.084	0.350 0.265	-0.009 0.978	0.392 0.207
Thirteen-lined ground squirrel M_{t+1}	-0.026 0.937	0.353 0.261	0.095 0.768	0.443 0.149	-0.134 0.678	0.425 0.169	0.444 0.148	-0.019 0.955	0.014 0.965	0.095 0.769	-0.007 0.983	-0.163 0.612	0.381 0.222	-0.781 0.003	-0.243 0.446
Meadow jumping mouse M_{t+1}	0.027 0.935	0.665 0.018	-0.109 0.736	0.424 0.170	-0.458 0.135	-0.269 0.398	0.401 0.197	-0.230 0.473	-0.487 0.109	0.263 0.410	-0.316 0.317	-0.370 0.236	0.605 0.037	-0.378 0.225	0.171 0.596
Masked shrew M_{t+1}	0.239 0.454	0.272 0.392	0.058 0.858	0.243 0.447	-0.054 0.866	0.135 0.677	0.586 0.045	-0.395 0.203	-0.294 0.353	0.479 0.115	-0.465 0.128	-0.370 0.236	0.476 0.117	-0.348 0.268	-0.102 0.753
Deer mouse M_{t+1}	-0.426 0.167	0.662 0.019	0.277 0.384	0.494 0.103	-0.127 0.693	0.405 0.192	0.549 0.064	-0.192 0.549	-0.015 0.964	0.235 0.462	-0.207 0.518	-0.472 0.121	0.685 0.014	-0.738 0.006	-0.036 0.911
Franklin's ground squirrel M_{t+1}	-0.356 0.256	0.864 < 0.001	0.112 0.729	0.430 0.162	-0.064 0.844	0.208 0.517	0.736 0.006	-0.349 0.266	0.030 0.927	0.424 0.169	-0.408 0.188	-0.416 0.179	0.585 0.046	-0.792 0.002	0.209 0.514
Total small mammal M_{t+1}	0.000 1.000	0.490 0.106	-0.336 0.286	0.162 0.616	-0.007 0.983	-0.130 0.688	0.193 0.548	-0.783 0.003	-0.217 0.499	0.829 0.001	-0.853 < 0.001	-0.583 0.047	0.434 0.159	-0.112 0.729	0.329 0.297
S	-0.026 0.936	0.644 0.024	0.140 0.665	0.470 0.124	-0.150 0.641	0.431 0.162	0.662 0.019	-0.345 0.272	0.021 0.947	0.421 0.173	-0.333 0.291	-0.464 0.129	0.590 0.043	-0.753 0.005	-0.107 0.740
E	0.154 0.634	-0.287 0.366	0.385 0.217	-0.025 0.940	-0.147 0.649	0.130 0.688	0.073 0.821	0.682 0.015	0.007 0.983	-0.705 0.011	0.748 0.005	0.453 0.139	-0.169 0.599	-0.081 0.804	-0.413 0.183
H'	0.000 1.000	0.392 0.208	0.357 0.255	0.359 0.253	-0.168 0.602	0.324 0.304	0.606 0.037	0.102 0.754	-0.070 0.829	-0.061 0.852	0.140 0.665	-0.065 0.842	0.497 0.100	-0.774 0.003	-0.308 0.331

Table 6. Spearman correlation coefficients (r_s) between the relative abundance (M_{t+1}) of small mammal species, species richness (S), evenness (E), and diversity (H') and macrohabitat-level soil moisture and vegetation characteristics sampled concurrently with small mammal surveys at 20 stratified random points in paired upland ($n = 11$) and wet-meadow ($n = 11$) habitats on Waterfowl Production Areas in Stutsman County, ND, in 2002. The probability of each observed bivariate correlation is indicated below the correlation coefficient. Biologically significant correlations ($r_s \geq |0.50|$) are indicated in bold.

	Habitat	Robel Visual Obstruction		Vegetation Height		Soil Moisture		% Grass Vegetation		% Forb Vegetation		% Woody Vegetation		% Litter		% Bare Ground		Litter Depth	
		Median	CV	Median	CV	Median	CV	Median	CV	Median	CV	Median	CV	Median	CV	Median	CV	Median	CV
Meadow vole M_{t+1}	0.279 0.208	0.041 0.855	-0.008 0.970	0.167 0.458	-0.046 0.840	0.521 0.013	-0.503 0.017	0.149 0.510	-0.152 0.500	0.171 0.447	-0.233 0.296	-0.148 0.512	0.013 0.853	-0.120 0.596	0.043 0.848	-0.017 0.939	-0.452 0.035	-0.032 0.887	-0.153 0.497
Thirteen-lined ground squirrel M_{t+1}	-0.266 0.231	-0.042 0.854	0.079 0.726	0.421 0.051	0.032 0.889	-0.220 0.326	0.067 0.766	0.146 0.518	-0.171 0.446	0.596 0.003	-0.466 0.029	-0.174 0.493	0.042 0.854	-0.589 0.004	0.445 0.038	0.155 0.490	0.200 0.373	-0.450 0.036	0.207 0.356
Meadow jumping mouse M_{t+1}	0.253 0.257	0.059 0.794	0.087 0.700	-0.097 0.669	0.428 0.047	-0.109 0.631	0.178 0.427	0.077 0.733	0.387 0.075	-0.006 0.980	0.009 0.968	0.074 0.742	0.143 0.525	-0.223 0.318	0.428 0.047	0.156 0.489	0.085 0.708	0.026 0.909	0.507 0.016
Masked shrew M_{t+1}	-0.326 0.138	0.089 0.694	0.465 0.029	0.193 0.390	0.050 0.824	-0.403 0.063	0.382 0.079	-0.009 0.968	0.069 0.762	0.390 0.073	-0.276 0.214	-0.134 0.553	0.391 0.072	-0.413 0.056	0.228 0.308	-0.052 0.817	0.308 0.163	-0.332 0.131	0.232 0.300
Deer mouse M_{t+1}	-0.160 0.476	0.155 0.490	0.220 0.324	0.312 0.158	0.028 0.901	-0.581 0.005	0.587 0.004	0.154 0.493	-0.075 0.740	0.231 0.301	-0.204 0.363	-0.140 0.534	0.119 0.599	-0.377 0.084	0.306 0.166	0.052 0.817	0.347 0.114	-0.032 0.889	0.353 0.107
Franklin's ground squirrel M_{t+1}	-0.137 0.543	0.101 0.654	-0.098 0.665	0.090 0.690	-0.066 0.770	-0.132 0.559	0.213 0.342	-0.116 0.606	0.190 0.397	0.448 0.036	-0.394 0.070	0.002 0.994	0.353 0.107	-0.299 0.177	0.212 0.343	-0.132 0.560	-0.073 0.747	0.023 0.919	-0.145 0.521
Total small mammal M_{t+1}	0.315 0.153	0.133 0.556	0.038 0.867	0.371 0.089	-0.033 0.883	0.430 0.046	-0.297 0.180	0.103 0.648	-0.097 0.667	0.458 0.032	-0.496 0.019	-0.270 0.225	0.187 0.406	-0.406 0.061	0.267 0.230	-0.120 0.594	-0.277 0.212	-0.080 0.723	-0.056 0.803
S	-0.251 0.259	-0.035 0.878	0.027 0.227	0.052 0.818	0.185 0.411	-0.422 0.050	0.427 0.048	-0.019 0.935	0.196 0.383	0.279 0.208	-0.279 0.209	-0.045 0.841	0.375 0.086	-0.360 0.100	0.425 0.048	0.036 0.875	0.257 0.249	-0.160 0.478	0.174 0.440
E	-0.193 0.388	0.037 0.869	-0.014 0.950	0.100 0.658	0.019 0.934	-0.527 0.012	0.474 0.026	0.141 0.531	-0.043 0.848	-0.030 0.893	0.168 0.455	0.031 0.890	-0.101 0.656	-0.154 0.494	0.094 0.678	0.017 0.939	0.289 0.192	0.010 0.963	0.241 0.280
H'	-0.279 0.208	-0.058 0.797	0.053 0.817	0.102 0.653	0.089 0.695	-0.595 0.004	0.477 0.025	0.245 0.273	0.028 0.903	0.140 0.533	-0.088 0.698	-0.063 0.782	0.037 0.871	-0.382 0.080	0.382 0.080	0.155 0.492	0.344 0.117	-0.033 0.883	0.322 0.143

Table 7. Spearman correlation coefficients (r_s) between the relative abundance (M_{t+1}) of small mammal species, species richness (S), evenness (E), and diversity (H') and macrohabitat-level soil moisture and vegetation characteristics sampled August 5-8, 2002, at 20 stratified random points in paired upland ($n = 11$) and wet-meadow ($n = 11$) habitats on Waterfowl Production Areas in Stutsman County, ND. The probability of each observed bivariate correlation is indicated below the correlation coefficient. Biologically significant correlations ($r_s \geq |0.50|$) are in bold.

	Habitat	Robel Visual Obstruction		Vegetation Height		Soil Moisture		% Grass Vegetation		% Forb Vegetation		% Woody Vegetation		% Litter		% Bare Ground		Litter Depth	
		Median	CV	Median	CV	Median	CV	Median	CV	Median	CV	Median	CV	Median	CV	Median ^a	CV	Median	CV
Meadow vole M_{t+1}	0.279	-0.013	0.284	-0.016	0.415	0.621	-0.327	0.189	0.142	-0.176	0.008	-0.223	0.119	-0.048	0.075	0.000	-0.175	-0.073	0.001
	0.208	0.955	0.212	0.946	0.061	0.003	0.148	0.413	0.541	0.444	0.973	0.332	0.608	0.836	0.746	1.000	0.449	0.752	0.996
Thirteen-lined ground squirrel M_{t+1}	-0.266	-0.086	-0.014	-0.041	0.174	0.025	-0.037	0.175	-0.163	-0.052	-0.048	0.110	-0.108	0.009	-0.143	0.000	0.083	-0.438	-0.037
	0.231	0.713	0.953	0.860	0.450	0.914	0.875	0.448	0.480	0.823	0.836	0.634	0.642	0.968	0.537	1.000	0.720	0.047	0.857
Meadow jumping mouse M_{t+1}	0.253	0.139	-0.033	0.197	-0.244	-0.037	0.041	-0.042	0.222	0.216	-0.103	0.291	0.100	-0.317	0.323	0.000	0.252	-0.280	0.086
	0.257	0.549	0.888	0.393	0.287	0.873	0.861	0.858	0.334	0.346	0.658	0.201	0.666	0.161	0.154	1.000	0.271	0.218	0.712
Masked shrew M_{t+1}	-0.326	-0.301	0.197	-0.191	0.220	-0.329	0.114	0.019	-0.035	-0.206	0.063	0.172	0.137	0.157	-0.250	0.000	-0.154	-0.500	-0.070
	0.138	0.186	0.392	0.406	0.337	0.145	0.623	0.934	0.881	0.371	0.788	0.455	0.555	0.498	0.274	1.000	0.504	0.021	0.762
Deer mouse M_{t+1}	-0.160	0.093	-0.084	0.125	-0.252	-0.320	0.152	-0.018	0.089	0.013	0.090	0.207	-0.202	0.082	0.115	0.000	0.457	-0.227	0.132
	0.476	0.688	0.718	0.589	0.270	0.157	0.510	0.937	0.701	0.955	0.699	0.367	0.380	0.724	0.620	1.000	0.037	0.323	0.569
Franklin's ground squirrel M_{t+1}	-0.137	0.052	-0.047	0.000	-0.180	-0.226	-0.010	-0.086	0.191	0.097	-0.012	0.305	0.316	-0.348	0.067	0.000	-0.177	0.170	-0.042
	0.543	0.822	0.839	1.000	0.435	0.325	0.967	0.712	0.406	0.675	0.958	0.179	0.163	0.122	0.774	1.000	0.443	0.460	0.858
Total small mammal M_{t+1}	0.315	0.034	0.187	0.003	0.290	0.509	-0.273	0.175	0.136	-0.028	-0.158	-0.113	0.167	-0.211	0.083	0.000	-0.217	-0.154	-0.062
	0.153	0.884	0.417	0.991	0.203	0.019	0.232	0.449	0.556	0.903	0.493	0.626	0.469	0.358	0.720	1.000	0.345	0.504	0.788
S	-0.251	0.003	0.055	0.114	-0.075	-0.226	-0.089	-0.046	0.148	0.043	-0.011	0.338	0.157	-0.095	0.109	0.000	0.193	-0.346	-0.004
	0.259	0.989	0.812	0.624	0.747	0.325	0.702	0.842	0.522	0.854	0.963	0.134	0.497	0.683	0.637	1.000	0.402	0.124	0.986
E	-0.193	0.018	-0.262	0.027	-0.307	-0.494	0.331	0.122	-0.249	0.075	0.165	0.055	-0.285	0.017	-0.097	0.000	0.376	0.045	0.008
	0.388	0.938	0.251	0.908	0.176	0.023	0.143	0.598	0.276	0.746	0.475	0.811	0.210	0.942	0.675	1.000	0.093	0.848	0.973
H'	-0.279	-0.008	-0.132	0.141	-0.259	-0.445	0.235	0.003	0.022	0.088	0.104	0.193	-0.080	0.028	0.012	0.000	0.406	-0.212	0.105
	0.208	0.973	0.567	0.543	0.258	0.043	0.305	0.991	0.924	0.705	0.654	0.402	0.731	0.904	0.960	1.000	0.068	0.356	0.650

^a All median % bare ground values were equal to 0.

Table 8. Spearman correlation (r_s) between the presence of small mammal species at specific trap locations and soil moisture and vegetation characteristics sampled concurrently with removal surveys at 20 stratified random points in paired upland and wet-meadow habitats (total vegetation samples = 440) on Waterfowl Production Areas in Stutsman County, ND, in 2002. The probability of each observed bivariate correlation is indicated below the correlation coefficient. Biologically significant correlations ($r_s \geq |0.50|$) are indicated in bold.

	Habitat	Robel Visual Obstruction	Veg. Height	Soil Moisture	% Grass Veg.	% Forb Veg.	% Woody Veg.	% Litter	% Bare Ground	Litter Depth
Meadow vole	0.125 0.009	0.018 0.705	0.083 0.081	0.205 < 0.001	-0.023 0.634	0.091 0.056	-0.122 0.010	0.075 0.114	-0.030 0.535	0.150 0.002
Thirteen-lined ground squirrel	-0.062 0.193	0.028 0.557	0.090 0.060	-0.047 0.327	0.041 0.390	0.131 0.006	-0.035 0.470	-0.098 0.039	0.055 0.250	-0.067 0.161
Meadow jumping mouse	0.090 0.059	0.226 < 0.001	0.113 0.018	0.047 0.322	-0.003 0.943	-0.001 0.980	0.120 0.018	-0.100 0.036	0.023 0.630	-0.111 0.020
Masked shrew	-0.108 0.024	0.034 0.477	0.121 0.011	-0.101 0.034	0.025 0.597	0.130 0.006	0.038 0.430	-0.132 0.006	0.004 0.935	-0.997 0.037
Deer mouse	0.044 0.361	0.090 0.059	0.074 0.121	-0.017 0.730	-0.062 0.192	0.015 0.751	0.009 0.847	-0.032 0.504	0.067 0.159	-0.100 0.035
Franklin's ground squirrel	0.034 0.477	0.057 0.234	0.051 0.291	0.036 0.452	0.041 0.394	0.131 0.006	0.022 0.651	-0.080 0.095	-0.039 0.410	-0.006 0.894
Total small mammals	0.091 0.057	0.161 < 0.001	0.193 < 0.001	0.133 0.005	-0.004 0.930	0.199 < 0.001	-0.038 0.421	-0.100 0.035	0.040 0.408	0.010 0.827

Table 9. Spearman correlation (r_s) between the presence of small mammal species at specific trap locations and soil moisture and vegetation characteristics sampled August 5-8, 2002, at 20 stratified random points in paired upland and wet-meadow habitats (total vegetation samples = 440) on Waterfowl Production Areas in Stutsman County, ND. The probability of each observed bivariate correlation is indicated below the correlation coefficient. Biologically significant correlations ($r_s \geq |0.50|$) are indicated in bold.

	Habitat	Robel Visual Obstruction	Veg. Height	Soil Moisture	% Grass Veg.	% Forb Veg.	% Woody Veg.	% Litter	% Bare Ground	Litter Depth
Meadow vole	0.205 < 0.001	0.048 0.329	0.047 0.335	0.291 < 0.001	0.143 0.003	0.048 0.325	-0.195 < 0.001	-0.019 0.692	-0.068 0.165	0.082 0.094
Thirteen-lined ground squirrel	-0.035 0.469	-0.055 0.259	-0.031 0.526	-0.036 0.457	0.030 0.546	-0.051 0.297	0.029 0.550	-0.015 0.759	-0.035 0.481	-0.004 0.934
Meadow jumping mouse	0.047 0.336	0.075 0.123	0.059 0.232	0.096 0.050	-0.018 0.719	-0.003 0.947	-0.006 0.898	-0.040 0.419	0.120 0.014	-0.127 0.009
Masked shrew	-0.022 0.655	0.017 0.734	0.023 0.640	-0.001 0.977	-0.007 0.890	-0.005 0.916	0.053 0.280	-0.0003 0.995	-0.043 0.384	-0.040 0.419
Deer mouse	-0.089 0.070	-0.092 0.059	-0.039 0.422	-0.037 0.455	-0.056 0.252	-0.074 0.132	-0.003 0.956	0.093 0.053	0.111 0.024	-0.119 0.015
Franklin's ground squirrel	-0.054 0.272	0.088 0.073	0.098 0.046	0.068 0.161	0.127 0.009	-0.052 0.290	-0.042 0.389	-0.101 0.039	-0.018 0.710	-0.070 0.151
Total small mammals	0.170 < 0.001	0.029 0.547	0.042 0.394	0.260 < 0.001	0.125 0.011	-0.0002 0.997	-0.135 0.006	-0.017 0.724	-0.031 0.524	-0.032 0.511

Table 10. Multiple stepwise regression models predicting the relative abundance (M_{t+1}) of small mammal species, species richness (S), evenness (E), and diversity (H') as a function of macrohabitat-level soil moisture and vegetation characteristics sampled concurrently with small mammal surveys on Waterfowl Production Areas in Stutsman County, ND, in 2001.

Model	Coefficient	SE	t	P
Meadow vole M_{t+1}:				
Intercept	212.708	30.236	7.03	< 0.001
CV % Forb + Woody Vegetation	-1.110	0.286	3.89	0.003
(F = 15.12, df = 1, 11, P = 0.003, r^2 = 0.602)				
Thirteen-lined ground squirrels M_{t+1}:				
Intercept	20.665	5.233	3.95	0.003
Median Litter Depth	-1.963	0.697	2.81	0.018
(F = 7.92, df = 1, 11, P = 0.018, r^2 = 0.442)				
Meadow jumping mouse M_{t+1}:				
Intercept	3.667	0.711	5.16	< 0.001
Masked shrew M_{t+1}:				
Intercept	1.123	0.383	2.93	0.015
CV Soil Moisture	0.103	0.043	2.41	0.037
(F = 5.83, df = 1, 11, P = 0.037, r^2 = 0.368)				
Deer mouse M_{t+1}:				
Intercept	3.691	4.459	0.83	0.429
Median Soil Moisture	4.940	1.765	2.80	0.021
Median Litter Depth	-1.498	0.320	4.68	0.001
(F = 14.48, df = 2, 11, P = 0.002, r^2 = 0.763)				
Franklin's ground squirrel M_{t+1}:				
Intercept	4.972	2.338	2.13	0.071
Median Soil Moisture	-2.895	0.857	3.38	0.012
CV Soil Moisture	0.352	0.049	7.23	< 0.001
Median Litter Depth	-0.523	0.170	3.08	0.018
CV Litter Depth	0.172	0.038	4.48	0.003
(F = 31.21, df = 4, 11, P < 0.001, r^2 = 0.947)				
Total small mammal M_{t+1}:				
Intercept	243.126	30.234	8.04	< 0.001
CV % Forb + Woody Vegetation	-1.235	0.286	4.33	0.002
(F = 18.71, df = 1, 11, P = 0.002, r^2 = 0.652)				
Species Richness (S):				
Intercept	4.943	1.934	2.56	0.031
Median Soil Moisture	1.890	0.765	2.47	0.036
Median Litter Depth	-0.559	0.139	4.03	0.003
(F = 10.88, df = 2, 11, P = 0.004, r^2 = 0.707)				
Evenness (E):				
Intercept	0.232	0.044	5.32	< 0.001
CV % Forb + Woody Vegetation	0.002	0.0004	3.81	0.003
(F = 14.52, df = 1, 11, P = 0.003, r^2 = 0.592)				
Diversity (H'):				
Intercept	1.428	0.291	4.92	< 0.001
Median Litter Depth	-0.114	0.039	2.94	0.015
(F = 8.65, df = 1, 11, P = 0.015, r^2 = 0.464)				

Table 11. Multiple stepwise regression models predicting the relative abundance (M_{t+1}) of small mammal species, species richness (S), evenness (E), and diversity (H') as a function of macrohabitat-level soil moisture and vegetation characteristics sampled concurrently with small mammal surveys on Waterfowl Production Areas in Stutsman County, ND, in 2002.

Model	Coefficient	SE	t	P
Meadow vole M_{t+1}:				
Intercept	42.361	16.686	2.54	0.020
Median Soil Moisture	10.784	3.884	2.78	0.012
(F = 7.71, df = 1, 21, P = 0.012, r^2 = 0.278)				
Thirteen-lined ground squirrels M_{t+1}:				
Intercept	39.243	7.713	5.09	< 0.001
CV % Grass Vegetation	-0.126	0.043	2.90	0.009
Median Litter Depth	-2.602	0.720	3.62	0.002
(F = 8.38, df = 2, 21, P = 0.003, r^2 = 0.469)				
Meadow jumping mouse M_{t+1}:				
Intercept	-2.140	4.742	0.45	0.657
CV % Litter	0.299	0.115	2.61	0.017
(F = 6.83, df = 1, 21, P = 0.017, r^2 = 0.255)				
Masked shrew M_{t+1}:				
Intercept	4.410	1.581	2.79	0.012
Median Soil Moisture	-0.897	0.332	2.71	0.014
Median % Forb Vegetation	0.644	0.094	6.84	< 0.001
(F = 27.42, df = 2, 21, P < 0.001, r^2 = 0.743)				
Deer mouse M_{t+1}:				
Intercept	1.204	1.446	0.83	0.415
CV Soil Moisture	0.045	0.016	2.84	0.010
(F = 8.04, df = 1, 21, P = 0.010, r^2 = 0.287)				
Franklin's ground squirrel M_{t+1}:				
Intercept	0.014	0.527	0.03	0.979
Median % Forb Vegetation	0.204	0.042	4.85	< 0.001
(F = 23.51, df = 1, 21, P < 0.001, r^2 = 0.540)				
Total small mammal M_{t+1}:				
Intercept	58.955	18.195	3.24	0.004
Median Soil Moisture	9.127	3.817	2.39	0.027
Median % Forb Vegetation	2.518	1.085	2.32	0.032
(F = 5.44, df = 2, 21, P = 0.014, r^2 = 0.364)				
Species Richness (S):				
Intercept	5.074	0.422	12.02	< 0.001
Median Soil Moisture	-0.205	0.089	2.32	0.032
Median % Forb Vegetation	0.081	0.025	3.21	0.005
(F = 8.00, df = 2, 21, P = 0.003, r^2 = 0.457)				
Evenness (E):				
Intercept	0.597	0.035	17.04	< 0.001
Median Soil Moisture	-0.021	0.008	2.56	0.019
(F = 6.58, df = 1, 21, P = 0.019, r^2 = 0.248)				
Diversity (H'):				
Intercept	0.585	0.163	3.59	0.002
Median Robel Visual Obstruction	-0.296	0.071	4.17	< 0.001
CV Soil Moisture	0.005	0.001	5.70	< 0.001
Median % Woody Vegetation	0.041	0.015	2.75	0.014
CV % Litter	0.019	0.003	5.36	< 0.001
(F = 13.17, df = 4, 21, P < 0.001, r^2 = 0.756)				

Table 12. Multiple stepwise regression models predicting the relative abundance (M_{t+1}) of small mammal species, species richness (S), evenness (E), and diversity (H') as a function of macrohabitat-level soil moisture and vegetation characteristics sampled August 5-8, 2002, on Waterfowl Production Areas in Stutsman County, ND.

Model	Coefficient	SE	t	P
Meadow vole M_{t+1} :				
Intercept	7.910	22.604	0.35	0.730
Median Soil Moisture	12.495	3.603	3.47	0.003
(F = 12.03, df = 1, 20, P = 0.003, r^2 = 0.388)				
Thirteen-lined ground squirrels M_{t+1} :				
Intercept	14.845	3.622	4.10	< 0.001
Median Litter Depth	-1.334	0.629	2.12	0.047
(F = 4.50, df = 1, 20, P = 0.047, r^2 = 0.192)				
Meadow jumping mouse M_{t+1} :				
Intercept	-4.511	6.626	0.68	0.504
CV % Litter	0.327	0.147	2.22	0.039
(F = 4.93, df = 1, 20, P = 0.039, r^2 = 0.206)				
Masked shrew M_{t+1} :				
Intercept	6.190	1.913	3.24	0.004
Deer mouse M_{t+1} :				
Intercept	4.429	1.092	4.05	< 0.001
Franklin's ground squirrel M_{t+1} :				
Intercept	1.524	0.653	2.33	0.030
Total small mammal M_{t+1} :				
Intercept	44.776	24.779	1.81	0.087
Median Soil Moisture	11.084	3.950	2.81	0.011
(F = 7.88, df = 1, 20, P = 0.011, r^2 = 0.293)				
Species Richness (S):				
Intercept	4.703	0.337	13.94	< 0.001
Median % Woody Vegetation	0.131	0.054	2.45	0.024
(F = 5.99, df = 1, 20, P = 0.024, r^2 = 0.240)				
Evenness (E):				
Intercept	0.620	0.045	13.91	< 0.001
Median Soil Moisture	-0.025	0.007	3.61	0.002
CV % Bare Ground	0.0003	0.0001	2.80	0.012
(F = 9.17, df = 2, 20, P = 0.002, r^2 = 0.505)				
Diversity (H'):				
Intercept	1.194	0.170	7.02	< 0.001
Median Soil Moisture	-0.079	0.026	3.02	0.007
CV % Bare Ground	0.0009	0.0004	2.14	0.046
(F = 6.03, df = 2, 20, P = 0.010, r^2 = 0.401)				

Table 13. Stepwise logistic regression models predicting the presence of small mammal species at specific trap locations as a function of microhabitat-level soil moisture and vegetation characteristics sampled concurrently with small mammal surveys on Waterfowl Production Areas in Stutsman County, ND, in 2002.

Model	Coefficient	SE	Wald χ^2	P
Presence of meadow voles at a trap location:				
Intercept	-1.813	0.311	33.944	< 0.001
Soil Moisture	0.112	0.030	14.134	< 0.001
Litter Depth	0.082	0.031	6.802	0.009
$(r^2 = 0.073; \chi^2_{HL} = 10.203, df = 8, P = 0.251)$				
Presence of thirteen-lined ground squirrels at a trap location:				
Intercept	-2.580	0.186	191.770	< 0.001
Presence of meadow jumping mice at a trap location:				
Intercept	-3.610	0.339	113.477	< 0.001
Robel Visual Obstruction	0.231	0.065	12.583	< 0.001
% Woody Vegetation	0.026	0.009	7.739	0.005
$(r^2 = 0.107; \chi^2_{HL} = 11.079, df = 8, P = 0.197)$				
Presence of masked shrews at a trap location:				
Intercept	-3.612	0.413	76.398	< 0.001
Habitat ^a	-1.410	0.509	7.672	0.006
Vegetation Height	0.022	0.007	8.943	0.003
% Forb Vegetation	0.027	0.008	10.479	0.001
$(r^2 = 0.153; \chi^2_{HL} = 7.453, df = 8, P = 0.489)$				
Presence of deer mice at a trap location:				
Intercept	-4.412	0.475	86.319	< 0.001
Robel Visual Obstruction	0.208	0.082	6.421	0.011
$(r^2 = 0.050; \chi^2_{HL} = 12.078, df = 8, P = 0.148)$				
Presence of Franklin's ground squirrels at a trap location:				
Intercept	-2.553	0.656	15.143	< 0.001
% Litter	-0.029	0.014	4.468	0.035
$(r^2 = 0.062; \chi^2_{HL} = 11.997, df = 8, P = 0.151)$				
Presence of any small mammal at a trap location:				
Intercept	-0.997	0.242	16.970	< 0.001
Vegetation Height	0.018	0.006	9.872	0.002
Soil Moisture	0.089	0.030	8.974	0.003
% Forb Vegetation	0.014	0.006	5.011	0.025
$(r^2 = 0.091; \chi^2_{HL} = 8.961, df = 8, P = 0.346)$				

^a Categorical dummy variable coded 0 = upland habitat and 1 = wet-meadow habitat.

Table 14. Stepwise logistic regression models predicting the presence of small mammal species at specific trap locations as a function of microhabitat-level soil moisture and vegetation characteristics sampled August 5-8, 2002, on Waterfowl Production Areas in Stutsman County, ND.

Model	Coefficient	SE	Wald χ^2	P
Presence of meadow voles at a trap location:				
Intercept	-1.215	0.227	28.657	< 0.001
Soil Moisture	0.160	0.033	23.791	< 0.001
% Woody Vegetation	-0.035	0.014	6.213	0.013
$(r^2 = 0.142; \chi^2_{HL} = 5.650, df = 7, P = 0.582)$				
Presence of thirteen-lined ground squirrels at a trap location:				
Intercept	-3.367	0.272	153.450	< 0.001
Presence of meadow jumping mice at a trap location:				
Intercept	-2.500	0.485	26.617	< 0.001
Robel Visual Obstruction	0.160	0.070	5.298	0.021
Litter Depth	-0.175	0.073	5.714	0.017
$(r^2 = 0.075; \chi^2_{HL} = 9.875, df = 8, P = 0.274)$				
Presence of masked shrews at a trap location:				
Intercept	-2.944	0.224	172.961	< 0.001
Presence of deer mice at a trap location:				
Intercept	-3.367	0.272	153.450	< 0.001
Presence of Franklin's ground squirrels at a trap location:				
Intercept	-14.595	4.767	9.373	0.002
Habitat ^a	-7.494	2.935	6.522	0.011
Soil Moisture	0.953	0.452	4.438	0.035
% Grass Vegetation	0.116	0.042	7.841	0.005
$(r^2 = 0.538; \chi^2_{HL} = 1.303, df = 4, P = 0.861)$				
Presence of any small mammal at a trap location:				
Intercept	-0.840	0.193	18.943	< 0.001
Soil Moisture	0.167	0.031	29.194	< 0.001
$(r^2 = 0.095; \chi^2_{HL} = 4.174, df = 6, P = 0.653)$				

^a Categorical dummy variable coded 0 = upland habitat and 1 = wet-meadow habitat.

CHAPTER 4: GENERAL CONCLUSION

DISCUSSION

This research was designed to improve our ability to study complex predator-prey interactions between small mammals, nesting passerine and waterfowl species, and medium-sized predators in the Northern Great Plains. Two distinct aspects of small mammal population ecology were investigated. First, three methods of assessing small mammal abundance and diversity, mark-recapture, removal, and track tube surveys, were compared and evaluated. These methods often produced different conclusions about the abundance and diversity of small mammals on sampled areas. Removal surveys consistently detected more species, and captured more individuals of those species, than mark-recapture surveys. Track tube surveys generally detected common species captured during mark-recapture and removal surveys, but often failed to detect rare species. In addition, ground squirrels (*Spermophilus tridecemlineatus* and *S. franklinii*) were overrepresented and meadow voles (*Microtus pennsylvanicus*) were underrepresented in track tube surveys when compared to mark-recapture and removal surveys. Track tube surveys did exhibit advantages over mark-recapture and removal surveys. Track tubes were relatively lightweight and were less expensive and faster to implement in the field than mark-recapture or removal surveys. Track tube surveys were largely unaffected by weather conditions and reduced exposure of researchers to mammalian-transmitted diseases. Finally, track tube surveys, in contrast to mark-recapture (Slade 1991) and removal surveys (Sullivan et al. 2003), appear to have little or no effect on small mammal behavior or survival.

Regression models between population estimates (\hat{N}) generated from mark-recapture and removal survey data and track tube indices explained moderate levels of the variation in \hat{N} . However, wide 95% prediction intervals indicated that these regressions would have low precision when predicting small mammal abundance from new track tube index observations. Two similar studies have reported strong correlations between small mammal abundance and track tube indices (Drennan et al. 1998, Glennon et al. 2002). Neither of these studies, however, evaluated prediction intervals to assess the reliability of track tube indices used to predict small mammal abundance.

Second, small mammal–habitat associations were investigated between upland and wet-meadow habitats (macrohabitat) and within upland and wet-meadow habitats (microhabitat). At the macrohabitat level, soil moisture and litter depth were commonly correlated with the relative abundance of small mammal species. At the microhabitat level, there were few strong correlations between soil moisture and vegetation characteristics and the presence of small mammals at specific trap locations. A subset of soil moisture and vegetation characteristics were found to be important in models predicting small mammal relative abundance, diversity, and distribution. Important soil moisture and vegetation characteristics identified in correlation analyses, such as soil moisture, median litter depth, and % forb vegetation, were often included in macrohabitat-level predictive models. These models generally explained moderate amounts of the variation in small mammal relative abundance and diversity. In contrast, predictive microhabitat models generally explained only a small proportion of the variation in the distribution of small mammal species as a function of soil moisture and vegetation characteristics sampled at specific trap locations. Morris (1987) and Jorgensen and Demarais (1999) suggested that when suitable microhabitat conditions are available in all macrohabitats, the effect of microhabitat conditions on small mammal distributions may be minimized. Instead, they proposed that macrohabitat-level vegetation characteristics were more influential on the relative abundance, diversity, and distribution of small mammals (Morris 1987, Jorgensen and Demarais 1999). Alternatively, it is possible that small mammal–habitat associations may be suppressed in relatively uniform grassland habitats such as those commonly found on Waterfowl Production Areas (WPAs). Soil moisture and vegetation characteristics differed much more between WPAs than between paired upland and wet-meadow habitats within WPAs, most likely because of previous land use and current management regimes that homogenize localized areas of habitat. Nonetheless, these correlation and regression analyses suggest that small mammals are responding to gradients in soil moisture and vegetation characteristics on WPAs, although relationships between small mammal relative abundance, diversity, and distribution do not seem to be as prominent as in other habitats (Bellows et al. 2001, McShea et al. 2003) or in native grasslands (Birney et al. 1976, Snyder and Best 1988).

In addition to investigating the primary objectives detailed above, the small mammal survey data collected during this research provides an opportunity to estimate the small mammal prey biomass available to predators in upland and wet-meadow grassland habitats. Biomass estimates were determined for each trapping grid by multiplying the small mammal naïve density times the mean live weight of each species. Naïve densities were calculated by dividing the removal survey population estimate (\hat{N}) by the area of the trapping grid (1.05 ha). Mean live weights for each species were calculated from data collected during small mammal surveys. This method undoubtedly generates biomass estimates that are biased high because of the known bias of naïve density estimates (Otis et al. 1978). In addition, combining juvenile and adult weights to create a mean weight for each species creates additional bias of unknown magnitude and direction. Nonetheless, these estimates provide a useful approximation of the small mammal prey biomass available to predators in these grassland habitats.

Total small mammal biomass averaged approximately 4,950 g live weight/ha in upland habitats, and 5,620 g live weight/ha in wet-meadow habitats (Table 1). Meadow voles, on average, contributed over half of the small mammal biomass in both habitats, with thirteen-lined ground squirrels and Franklin's ground squirrels making up the majority of the remaining biomass (Table 1). Grant et al. (1977) reported similar maximum total small mammal biomass estimates of approximately 4,100 g live weight/ha in Colorado grasslands treated with supplemental water and nitrogen. Grant and Birney (1979), however, reported total small mammal biomass estimates of only 300 g live weight/ha from southwestern North Dakota grasslands.

Further insight into grassland predator-prey interactions can be gained by comparing these small mammal biomass estimates with biomass estimates of other available prey items. Higgins et al. (1992) reported average waterfowl pair densities of 0.4 pairs/ha, or 0.8 adult waterfowl/ha, in central North Dakota grasslands. Blue-winged teal (*Anas discors*), gadwall (*A. strepera*), and mallards (*A. platyrhynchos*) make up over 70% of nesting waterfowl in central North Dakota (Higgins et al. 1992), and together have a mean adult weight during the breeding season of approximately 755 g (Lokemoen et al. 1990), which results in a

conservative estimate of adult waterfowl biomass of approximately 604 g live weight/ha. If each waterfowl pair produces an average clutch of 9.77 eggs (Higgins et al. 1992), with average egg weights of 39.9 g (Lokemoen et al. 1990), then a conservative estimate of egg biomass available to predators is approximately 156 g/ha. Biomass estimates can also be generated for passerine species. Wiens and Dyer (1975) reported that total passerine biomass in mixed-grass prairies averaged 99.5 g live weight/ha. Risser et al. (1981:222) reported total passerine biomass estimates of 143.3 g live weight/ha for grasslands in Stutsman County, North Dakota. These estimates yield a combined passerine and waterfowl biomass of approximately 900 g live weight/ha in grassland habitats similar to those surveyed during this research.

Although simplified and most likely biased, these estimates provide a useful approximation of available prey biomass and suggest that small mammals make up a much larger proportion of total prey biomass in central North Dakota grassland habitats than avian species and their nests. More research is necessary, however, before definitive conclusions can be made about the role of small mammals in predator-prey interactions. For example, invertebrates are consumed by most medium-sized grassland predators, and are the primary prey item in the diets of striped skunks (*Mephitis mephitis*; Greenwood et al. 1999). Unfortunately, invertebrate biomass is difficult to quantify and remains a little studied aspect of grassland predator-prey systems. In addition, foraging predators and potential prey utilize habitats, such as roadsides and agricultural fields, not surveyed during this research. Both predator foraging activities (Kuehl and Clark 2002, Phillips et al. 2003) and avian abundance and nesting success (Cowardin et al. 1985, Klett et al. 1988, Best et al. 1997) have been studied in these habitats. Much less is known, however, about small mammal abundance and diversity in roadsides and agricultural lands. Prey availability also varies temporally. For part of each year, avian species and their nests are unavailable to predators, whereas small mammals are generally available throughout the year in grassland habitats. Ultimately, our understanding of predator-prey interactions is contingent upon improved knowledge of the spatial and temporal variability of different prey items and the interaction between prey abundance and predator foraging activities at multiple scales.

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Table 1. Estimated small mammal biomass (g live weight/ha) in upland and wet-meadow habitats on Waterfowl Production Areas in Stutsman County, ND, 2001-2002. Number of sampled sites (n) indicated for each biomass estimate.

	Habitat	n	Biomass	SE
All small mammals	Upland	19	4,948.07	659.38
	Wet Meadow	15	5,616.78	778.26
	Habitats Combined	34	5,252.03	499.90
Without squirrels	Upland	19	2,793.14	423.07
	Wet Meadow	15	4,256.62	838.07
	Habitats Combined	34	3,433.41	448.41
Vole	Upland	19	2,718.40	427.10
	Wet Meadow	15	4,004.20	790.16
	Habitats Combined	34	3,299.08	434.95

APPENDIX: SUMMARY OF MARK-RECAPTURE, REMOVAL, AND TRACK TUBE SURVEYS

Summary of species richness (S), number of unique individuals captured (M_{t+1}), population estimates (\hat{N}), and track tube indices (number of track tubes with identifiable tracks) for small mammal surveys conducted on Waterfowl Production Areas in Stutsman County, ND, 2001-2002.

All small mammals

WPA	Habitat	Mark-Recapture Surveys				Removal Surveys				Track Tube Surveys	
		S	M_{t+1}	\hat{N}_{MR}	SE	S	M_{t+1}	\hat{N}_{REM}	SE	S	Track Tube Index
Cottonwood Lake (2001)	upland	4	112	191	15.73	3	113	129	8.08	1	138
	wet meadow	2	146	280	19.45	4	158	214	24.35	3	211
Gaier (2001)	upland	3	8	12	5.48	4	47	54	5.66	a	a
	wet meadow	3	8	17	5.02	4	44	109	89.97	a	a
Strand (2001)	upland	6	77	163	15.27	7	122	144	10.68	4	91
	upland	4	89	191	16.37	7	148	198	38.06	4	89
	upland	3	37	81	10.74	5	129	157	13.22	4	82
	wet meadow	4	13	28	6.36	8	86	190	91.65	4	254
Woodworth Station (2001)	upland	3	105	196	16.14	5	155	218	58.67	4	209
	upland	5	81	164	15.13	6	212	321	43.85	3	144
Zimmerman II (2001)	upland	2	21	36	6.63	3	64	97	24.36	2	34
	wet meadow	3	47	107	12.50	4	159	469	262.35	3	64
Beck (2002)	upland	3	22	50	8.45	7	135	219	45.15	4	132
	wet meadow	3	27	45	10.06	3	151	176	13.60	2	24
Chase Lake (2002)	upland	5	33	68	9.80	5	80	122	27.81	5	77
	wet meadow	5	70	120	12.46	5	139	193	25.53	3	118
	upland	4	49	78	9.59	6	105	130	12.91	3	55
	wet meadow	4	98	199	16.65	3	179	210	12.28	4	82
Major (2002)	upland	3	14	31	6.69	3	48	69	17.88	2	15
	wet meadow	5	88	180	15.85	5	148	157	5.64	4	330
Mud Lake (2002)	upland	6	90	190	16.25	5	226	283	20.12	4	222
	wet meadow	4	120	228	17.47	6	244	342	36.35	4	237
Mt. Moriah (2002)	upland	8	30	63	9.26	9	87	108	11.85	5	180
	wet meadow	6	38	65	9.05	8	115	126	7.07	6	296
Peda (2002)	upland	2	6	6	2.04	4	36	40	4.50	3	27
	wet meadow	2	9	14	5.81	4	33	53	25.06	1	25
Theisen Marsh (2002)	upland	4	13	28	6.36	6	27	46	22.55	3	15
	wet meadow	3	3	3	3.35	4	26	50	38.97	2	4
	upland	5	44	97	11.88	5	103	132	15.44	2	70
	wet meadow	5	42	95	11.74	5	102	131	15.41	4	73
Woodworth Station (2002)	upland	5	19	43	7.95	5	41	b	b	3	36
	wet meadow	3	12	22	5.18	5	56	112	55.30	3	26
	upland	3	59	75	5.88	4	88	100	6.91	3	137
	wet meadow	5	105	187	15.65	3	182	249	27.53	3	161

^a Track tube surveys not conducted.

^b Non-estimable with Model M_{bh} in Program CAPTURE.

Without squirrels

WPA	Habitat	Mark-Recapture Surveys				Removal Surveys				Track Tube Surveys	
		S	M_{t+1}	\hat{N}_{MR}	SE	S	M_{t+1}	\hat{N}_{REM}	SE	S	Track Tube Index
Cottonwood Lake (2001)	upland	3	110	186	15.47	2	112	128	8.31	1	138
	wet meadow	2	146	280	19.45	3	157	213	24.35	2	210
Gaier (2001)	upland	2	6	9	4.74	3	44	51	5.88	a	a
	wet meadow	2	5	8	2.96	3	38	b	b	a	a
	upland	4	69	150	14.67	5	100	127	14.58	2	31
	upland	3	85	181	15.90	5	127	148	9.93	2	73
Strand (2001)	upland	2	36	78	10.56	3	122	151	13.83	2	21
	wet meadow	3	10	16	6.12	6	64	193	177.02	2	3
Woodworth Station (2001)	upland	2	102	188	15.79	3	145	205	58.93	2	105
	upland	4	80	162	15.01	4	198	309	47.41	1	45
Zimmerman II (2001)	upland	2	21	36	6.63	2	63	93	22.23	2	34
	wet meadow	2	46	104	12.35	3	157	522	349.83	1	58
Beck (2002)	upland	3	22	50	8.45	5	128	192	32.82	3	36
	wet meadow	3	26	44	9.87	3	151	176	13.60	2	24
Chase Lake (2002)	upland	4	31	62	9.41	4	68	147	77.08	4	75
	wet meadow	4	66	112	11.98	4	130	191	31.03	1	97
	upland	3	40	52	5.64	5	83	114	18.98	2	41
	wet meadow	4	96	194	16.42	2	178	208	11.94	4	81
Major (2002)	upland	2	13	29	6.41	3	48	69	17.88	2	15
	wet meadow	4	86	175	15.61	3	134	142	5.57	3	136
Mud Lake (2002)	upland	4	82	170	15.30	3	208	271	23.56	2	148
	wet meadow	3	119	225	17.36	5	231	331	38.90	3	198
Mt. Moriah (2002)	upland	7	20	40	7.23	7	62	76	9.47	3	51
	wet meadow	4	29	51	7.99	6	92	99	5.33	4	65
Peda (2002)	upland	2	6	6	2.04	3	31	34	3.54	2	25
	wet meadow	1	8	12	5.48	3	30	53	31.51	1	25
Theisen Marsh (2002)	upland	3	11	22	5.61	4	24	72	107.73	2	6
	wet meadow	3	2	4	2.74	4	26	50	38.97	2	4
	upland	3	40	87	11.23	4	85	109	13.91	1	33
	wet meadow	4	41	92	11.58	4	95	127	17.81	3	56
Woodworth Station (2002)	upland	4	13	21	6.98	4	38	b	b	2	8
	wet meadow	2	11	22	5.61	4	52	98	45.78	2	20
	upland	3	59	75	5.88	3	69	76	5.08	2	117
	wet meadow	4	101	179	15.30	2	169	238	29.67	2	134

^a Track tube surveys not conducted.^b Non-estimable with Model M_{bh} in Program CAPTURE.

Vole

WPA	Habitat	Mark-Recapture Surveys			Removal Surveys			Track Tube Surveys
		M_{t+1}	\hat{N}_{MR}	SE	M_{t+1}	\hat{N}_{REM}	SE	Track Tube Index
Cottonwood Lake (2001)	upland	107	178	15.06	108	125	9.03	138
	wet meadow	136	257	18.57	143	194	23.53	209
Gaier (2001)	upland	4	5	3.87	40	45	4.90	a
	wet meadow	3	3	3.35	34	b	b	a
	upland	64	139	14.15	83	98	8.84	23
	upland	73	156	14.81	110	122	6.55	52
Strand (2001)	upland	34	77	10.57	110	141	15.71	14
	wet meadow	4	5	3.87	49	161	191.65	1
Woodworth Station (2001)	upland	102	188	15.79	137	191	56.62	104
	upland	74	150	14.51	181	254	30.23	45
Zimmerman II (2001)	upland	19	34	6.49	60	83	16.88	25
	wet meadow	45	102	12.20	153	455	263.36	58
Beck (2002)	upland	17	41	7.75	107	132	13.02	30
	wet meadow	25	42	9.68	141	168	15.44	22
Chase Lake (2002)	upland	21	39	7.30	54	84	24.41	5
	wet meadow	22	44	7.92	89	143	35.30	0
	upland	21	32	5.58	45	49	3.49	3
	wet meadow	94	191	16.31	169	190	8.97	79
Major (2002)	upland	10	21	5.44	43	59	14.23	8
	wet meadow	68	136	13.72	93	96	3.00	133
Mud Lake (2002)	upland	78	162	14.93	189	235	17.86	137
	wet meadow	112	211	16.82	205	279	28.91	197
Mt. Moriah (2002)	upland	4	8	3.19	4	b	b	0
	wet meadow	10	12	2.75	18	27	12.30	0
Peda (2002)	upland	4	5	2.21	23	24	2.48	23
	wet meadow	8	12	5.48	25	47	34.92	35
Theisen Marsh (2002)	upland	5	8	2.96	12	15	4.92	2
	wet meadow	1	1	1.00	19	25	9.40	3
	upland	38	84	11.07	73	89	10.29	33
	wet meadow	27	61	9.45	66	72	4.55	50
Woodworth Station (2002)	upland	9	14	5.81	29	b	b	6
	wet meadow	10	22	5.78	46	98	60.33	18
	upland	56	69	5.26	59	61	2.35	116
	wet meadow	98	174	15.06	168	237	29.71	133

^a Track tube surveys not conducted.

^b Non-estimable with Model M_{bh} in Program CAPTURE.

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