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MUSEUM COLLECTIONS OF MAMMALS CORROBORATE THE EXCEPTIONAL DECLINE OF PRAIRIE HABITAT IN THE CHICAGO REGION

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The prairie deer mouse (*Peromyscus maniculatus bairdii*) was more common than the white-footed mouse (*P. leucopus*) in museum collections from the 6 Illinois counties of the Chicago region before 1920 but constitutes only 5% of specimens deposited since 1970. Because white-footed mouse prefers woody vegetation and because prairie deer mouse is limited to prairie or large open habitats, the change in proportion is likely driven by a disproportionate loss of prairie among remaining natural habitat and increases in woody vegetation within grasslands. The decline of the prairie vole (*Microtus ochrogaster*) relative to the meadow vole (*M. pennsylvanicus*) and the lack of recent specimens of Franklin's ground squirrel (*Spermophilus franklinii*) corroborate the hypothesis that prairie habitats have declined much more so than wooded habitats in the Chicago region. Based on extinction models using museum records, it is probable that *S. franklinii* is already locally extirpated. Regression analysis suggests the white-footed mouse will be the only local *Peromyscus* in 0–140 years.

Key words: local extinction, *Microtus, Peromyscus,* prairie deer mouse, prairie loss, prairie vole, *Spermophilus franklinii*

While few would deny the enormous impact of human economic activities during the last 200 years on fauna and flora, documentation is not always easy to find (Whitney 1994). Knowledge of the extent of change is lessened by biologists' tendency to sample places that have undergone the least change, natural areas and preserves. Even in a highly urbanized area such as northeastern Illinois, it is possible to find natural areas to trap mammals. Although natural areas still exist in the Chicago region, the proportion of natural habitat that is prairie has declined relative to woodland (Iverson et al. 1989). Museum collections of local rodents reveal a temporal decline in the proportion of prairie species relative to generalist species in the same genus, corroborating the disproportionate loss of prairie habitat.

Our interest in obtaining DNA of historic specimens of *Peromyscus* to study the genetic effects of habitat loss and fragmentation led us to assemble a list of museum specimens of *P. leucopus* and *P. maniculatus* from 6 counties (Cook, DuPage, Kane, Lake, McHenry, and Will) in northeastern Illinois, known as the Chicago region. As the information about the specimens available in museums was assembled, it was apparent that collections before 1900 contained a much higher proportion of *P. maniculatus* compared with *P. leucopus,* whereas the reverse was true in more recent collections. To understand this change, we studied the habitats of these 2 species, which are represented in this area by the subspecies *P. maniculatus bairdii* and *P. leucopus noveboracensis.*

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Hoffmeister (1989) described *P. maniculatus bairdii* as closely associated with prairie habitats whereas *P. leucopus noveboracensis* was associated with woodlands. Knowledge of these 2 species in the Chicago region began with Robert Kennicott, who in 1857 wrote ''The [prairie deer mouse] is found abundantly on the prairies in Northern Illinois and Southern Wisconsin. . . . It is strictly an inhabitant of the prairies, where it replaces the [white-footed mouse]. I have never observed it in the woods, even near prairie fields where it abounds. In Northern Illinois and Southern Wisconsin, this [prairie deer mouse] is a much more numerous species than the [white-footed mouse]'' (Kennicott 1857: 664). Other early reports (Cory 1912; Gregory 1936; C. C. Sanborn, in litt.) confirm the prairie and woodland habitat separation originally reported by Kennicott.

If the local decline of the prairie deer mouse relative to the white-footed mouse that we observed in museums is due to the greater loss of prairie compared with woodland habitat in the Chicago region, then other mammals inhabiting prairies are also expected to have experienced relatively large declines in abundance. As with *Peromyscus*, the genus *Microtus* locally has a pair of common species with 1 species, the prairie vole (*M. ochrogaster*) found primarily in prairies and another, the meadow vole (*M. pennsylvanicus*), with much broader habitat affinities. Comparison of the proportion of the prairie species to other species in the same genus is the central part of our study. For Franklin's ground squirrel (*Spermophilus franklinii*) there was no woodland member of the genus and we could only evaluate its decline with single-species techniques.

Materials and Methods

Inquiries were sent to 18 museums in the United States and Europe inquiring about their holdings of specimens of *P. maniculatus* and *P. leucopus,* collected from 6 northeastern Illinois counties (Cook, DuPage, Kane, Lake, McHenry, and Will), which we define as the Chicago region (Appendix I). We tabulated each specimen by species, subspecies, museum of residence, county where collected, collector, and year in which collected.

We consulted 7 regional mammal references (Burt 1948; Gregory 1936; Hoffmeister 1989; Jackson 1961; Jones et al. 1985; Kurta 1995; Schwartz and Schwartz 1981) to identify other prairie mammals (Appendix I). If a majority of authors stated that a particular mammal species preferred a prairie habitat to other habitats, and the species' geographic distribution as described by Hoffmeister (1989) included any part of the 6-county Chicago region, we included that species in our list of local prairie mammals.

Because 3 Illinois museums had >89% of the specimens of *Peromyscus* from the Chicago region, we requested collection information about the other prairie mammals only from those collections, except for *S. franklinii* for which we recontacted all 18 museums.

In recent decades fewer specimens of common species may have been collected from already represented areas. We evaluated this hypothesis by tabulating the number of specimens of *Peromyscus* and *Microtus* as a function of time. Because some species of *Peromyscus* are difficult to identify (Hoffmeister 1989; Rich et al. 1996; Sternburg and Feldhamer 1997), we reevaluated all *Peromyscus* that were available at the Field Museum (including 28 on loan from other museums). Diagnostics used to identify *P. leucopus* or *P. maniculatus* were those recommended by Hoffmeister (Hoffmeister 1989; Hoffmeister and Mohr 1957). Hind foot length and tail length were taken from museum tags. Zygomatic width of skull and crown length of maxillary toothrow were measured with a digital caliper to the nearest 0.1 mm. Intermediate values, namely, hind foot measurements of 18 or 19 mm, zygomatic width of skull measurements of 11.9–12.1 mm, and a crown length of maxillary toothrow measurement of 3.3 mm were deemed to be inconclusive, and not used.

Two approaches were used to understand the temporal change of species composition within a genus. First, we divided the entire time period into 6 intervals (1850–1899, 1900–1919, 1920–1939, 1940–1959, 1960–1979, and 1980–1999) selected by compromising between a desire for uniform time periods and a minimum of 20 individuals/interval. For each time period, we cal-

culated the proportion of prairie species among the pair of species within the genus. We named the variables PPPero for proportion of prairie *Peromyscus* (=numbers of *P. maniculatus*/[numbers of *P. maniculatus* + *P. leucopus*]) and PPMicro, for proportion of prairie *Microtus*, (=numbers of *M. ochrogaster*/[numbers of *M. ochrogaster* + *M. pennsylvanicus*]). Each variable was graphed using the 6 time intervals. The standard deviation for each interval was calculated according to the binomial method described by Newcombe (1998). Second, we calculated the same variables, PPPero and PPMicro for each year between 1850 and 1996, the 1st and last years included in our records, in which ≥1 specimen of the genus from the Chicago region was deposited. The number of specimens in each genus collected in these years varied greatly (*Peromyscus* range, 1–196; *Microtus* range, 1–477). Many years had no deposited individuals. The null hypothesis was that PPPero and PPMicro were not changing through time.

We used linear regression to estimate the rates of decline of prairie mammals *P. maniculatus* and *M. ochrogaster* in relation to woodland/generalist species in the same genus, *P. leucopus* and *M. pennsylvanicus*, respectively. In the regression we set the year 1840 as the estimator of the original (=presettlement) proportions because public land surveys of the region were completed in that year (G. Nyberg and D. Nyberg, in litt.). The regression slope estimates the rate of change with time in PPPero and PPMicro. The year when PPPero = 0 estimates when *P. maniculatus* would be locally extinct. A confidence interval (95%) for the independent variable (year) when the dependent variable (PPPero or PPMicro) = 0 was calculated by solving the inverse regression (Draper and Smith 1998). The regression and other statistical analyses were done with SYSTAT v. 9 (SPSS, Inc. 2000).

The rate of loss of prairie habitat and the proportion of natural area that was prairie (prairie divided by prairie plus woodlands) between 1840 and 1976 were estimated from data in Iverson et al. (1989) and White (1978).

McCarthy (1998) reviewed and evaluated methods of estimating the decline of a species from museum records and concluded that the equation of Solow (1993) was the most useful of the methods reviewed. This equation attempts to estimate the probability that the most recent collection date would be when it was observed (or earlier) given the null hypothesis that the species is still extant. The probability that a species is still extant equaled the number of years between the 1st record and the last specimen record divided by the number of years between the 1st record and the last catch that could have included the species in question (1996 in our study), raised to the power of the number of ''catch efforts'' or times when the species was caught (McCarthy 1998).

Results

A total of 703 *P. maniculatus* and *P. leucopus* specimens from the Chicago region were found in 14 museums. Specimens were collected in Cook (n = 377), DuPage (61), Kane (35), Lake (162), and Will (68) counties. No specimen was collected in McHenry County. Collections of *Peromyscus* ranged from 1855 to 1996 with 116 specimens labeled *P. maniculatus* and 587 specimens labeled *P. leucopus* (2 were excluded as they lacked date of collection).

Identification of *Peromyscus* specimens at the Field Museum or on loan to us was performed. Of a total of 490 specimens, 247 (50%) were not evaluated because the skull was not part of the collection (e.g., fluid preserved, was missing, or was broken so as to be unusable), and 20 specimens were eliminated as juveniles by examination of skull suture and pelage. The remaining 223 specimens included 189 specimens tagged *P. leucopus* and 34 specimens tagged *P. maniculatus*. Using the diagnostics recommended by Hoffmeister (1989), we found all 189 specimens labeled *P. leucopus* to be *P. leucopus*, but 6 of the 34 (17.6%) individuals labeled *P. maniculatus* were diagnosed as *P. leucopus* with the remaining 28 correctly classified. The 6 incorrect labels included one in each of the following years: 1900, 1926, 1936, 1975, 1976, and 1982.

We identified 4 Chicago region prairie mammals, including prairie vole, least shrew (*Cryptotis parva*), western harvest mouse (*Reithrodontomys megalotis*), and Franklin's ground squirrel. Only 1 specimen

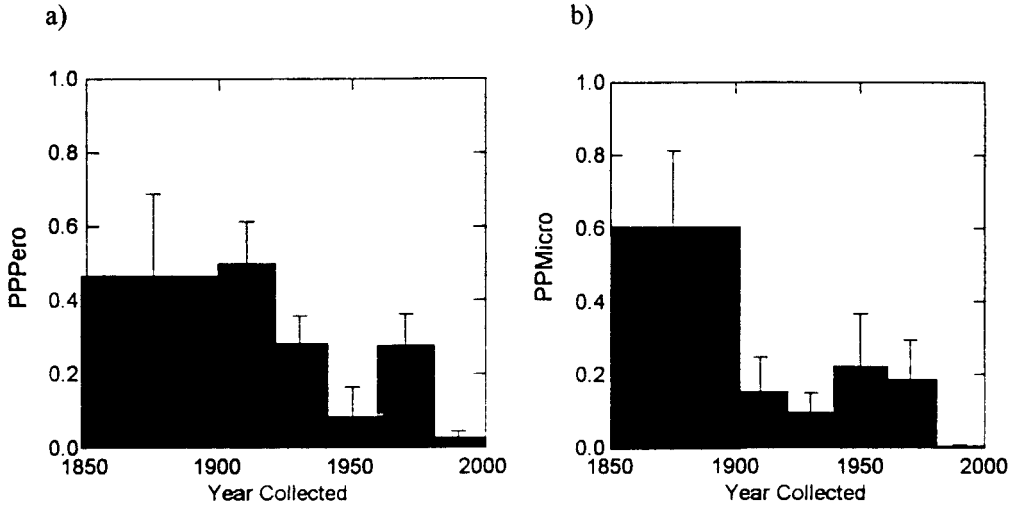

FIG. 1.—Proportions of a) prairie *Peromyscus* (PPPero) and b) prairie *Microtus* (PPMicro) in each of 6 time classes; error bars represent ≥1 *SD*.

of the least shrew and no specimens of the western harvest mouse from the Chicago region were located, so no further analysis was done on those species. The prairie vole and the meadow vole are a pair of species with some similarity to the pair of species of *Peromyscus*. *M. ochrogaster* is largely confined to prairies whereas *M. pennsylvanicus* is more common in meadows and scrub (Hoffmeister 1989).

We found 880 *M. ochrogaster* and *M. pennsylvanicus* specimens from the Chicago region. By county, specimens were collected in Cook (n = 535), DuPage (182), Kane (4), Lake (103), and Will (56). The range of years in which those specimens were collected was 1850–1995. By species, 44 specimens were *M. ochrogaster* and 836 specimens were *M. pennsylvanicus* (5 did not have the year collected).

The idea that museums have stopped acquiring *Peromyscus* and *Microtus* from well-collected regions is incompatible with the collection records unless the change has occurred in the last 10 years. Arbitrarily choosing 1971 (the last year *S. franklinii* was collected) as a year dividing the collections into ancient and recent, we found 310 *Peromyscus*, 231 *Microtus*, 42 *Spermophilus*, and 1 *Cryptotis*, or 584 specimens collected in 1971 or before, and 391 *Peromyscus* and 643 *Microtus*, or 1,034 specimens collected after 1971. The use of 1850–1996 as the range of collection years resulted in averages of 4.8 specimens/year collected before 1971 and 41.4 specimens/year collected after 1971.

Proportions of prairie species in each time interval indicated that in both cases, PPPero and PPMicro, the post-1980 proportions were lowest (Fig. 1). Prairie species were rarest in the most recent time interval. The highest proportion of prairie *Microtus*, PPMicro, was the earliest interval, 1850–1899; the highest value of PPPero was in the 2nd oldest interval, 1900–1919. For both variables there was a general decline with time, although the decrease was not monotonic in either case.

We used the data set in which PPMicro and PPPero were calculated for each year in regression analysis. Many years had a value of 0 or 1, and neither the original distribution nor the arcsine square root transformation were normally distributed according to the Lilliefors test (SPSS, Inc. 2000); therefore, untransformed data were

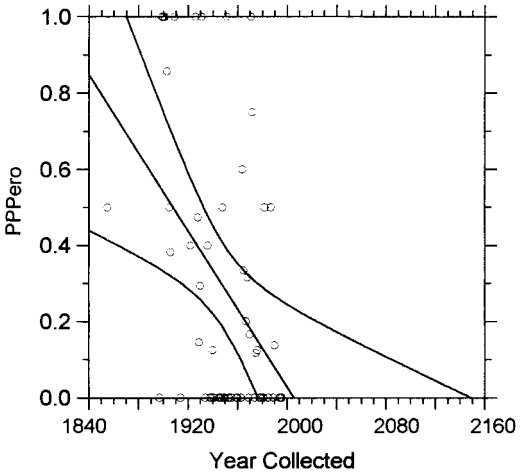

FIG. 2.—Linear regression of proportion of prairie *Peromyscus* (PPPero) against year collected.

used in the analysis (Draper and Smith 1998; Reyment 1972).

The result was a significant linear regression of PPPero relative to year (F = 12.662, *d.f.* = 1, 54; P = 0.001; Fig. 2). *Peromyscus* specimens were collected in 56 out of 142 possible years. PPPero = 0 in 26 years and PPPero = 1 in 8 years. PPPero intercepted the year 1840 at a value of 0.85, meaning that 85% of presettlement *Peromyscus* were estimated to be *P. maniculatus.* The 95% *CI* of that estimate was 0.44–1.00; slope was −0.005, meaning that the proportion of *P. maniculatus* was estimated to have declined 0.5%/year over the span of the observations. The year in which PPPero was estimated to equal zero predicted the year of local extinction of *P. maniculatus bairdii.* That year was 2009, with a 95% *CI* estimated by inverse regression of 1976–2149. The values presented above were based on the complete data set; the parameters estimated from the 223 individuals in the confirmed identification subset were an intercept of 0.83 and a slope of −0.006 (F = 34.251, *d.f.* = 1, 27; $P < 0.0005$), essentially the same.

Microtus specimens were collected in 46 of 146 possible years: PPMicro = 0 in 26 years and PPMicro = 1 in 3 years. For PPMicro, the 1840 intercept was 0.47, indicating that 47% of *Microtus* in the presettlement period are estimated to have been *M. ochrogaster*. The slope was −0.003, meaning the decline in the proportion *M. ochrogaster* was 0.3%/year, but the regression was not significant (F = 3.096, *d.f.* = 1, 44; P = 0.085). PPMicro's x-intercept was the year 1996, but the upper bound of the 95% *CI* did not intercept the x-axis, which was not surprising because the regression was not significant.

Values of the rates of declines in the proportion of prairie mammals to the rate of decline of prairie habitat in the region are similar. The proportion of the 6-county area that was prairie in 1840 was 0.76, and the proportion of terrestrial habitat that was prairie (prairie/[prairie + woodland]) was 0.81 (Iverson et al. 1989). In 1980, the proportion of the terrestrial habitat that was prairie (open grassland/[open grassland + woodland]) was 0.42 for the 6-county area (Iverson et al. 1989). White (1976) estimated that <0.1% of the original prairie remained covered by native vegetation. In Fig. 3 the PPPero and PPMicro linear regression lines are graphed along with a line connecting the proportion of the landscape that was native prairie in 1840 and 1976 and a line connecting the prairie proportion of terrestrial habitat in 1840 and 1980. The slope of the latter line was −0.003. The slope of the line connecting the 2 points of the prairie loss line was −0.005/year.

Forty-two specimens of *S. franklinii* collected in the Chicago region were found in 8 museums: Cook (19), DuPage (6), Kane (5), Lake (9), and Will (3). The range of years in which those specimens were collected was 1855–1971. There were 20 successful catch efforts recorded for *S. franklinii.*

Probabilities that the last collection of a species would be when it was (or earlier) given the hypothesis that the species was extant as calculated with Solow's equation (Solow 1993) were: *M. ochrogaster* (0.61),

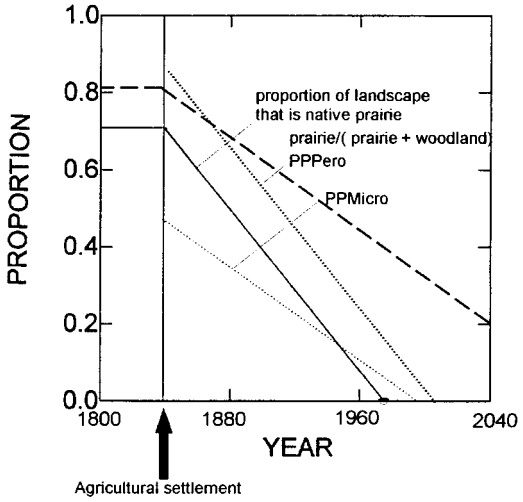

FIG. 3.—Changes of vegetation variables and mammalian species composition variables with time. Comparison of proportion of native prairie in the landscape and the proportion of treeless terrestrial vegetation with PPPero and PPMicro. All 4 variables have declined between 0.3% and 0.5% per year.

M. pennsylvanicus (0.74), *P. leucopus* (1.00), *P. maniculatus* (0.37), and *S. franklinii* (0.02). The *P*-value of 1.00 for *P. leucopus* was because it was collected in the last observation year for all species, 1996.

DISCUSSION

Collecting practices of naturalists are likely to underestimate the extent of change of plants and animals at the landscape level by deliberately avoiding human altered areas (Resetar 1998). As long as species persist in the remaining natural areas, specimens continue to be deposited in collections. Indeed, the number of specimens of the 4 species of *Peromyscus* and *Microtus* deposited since 1971, the last year a Franklin's ground squirrel was deposited, far exceeds the number deposited before that time, despite a dramatic decline in natural areas in this metropolitan region. In Cook County, for example, 61.5% of the county was covered by urban land in 1995 (Illinois Department of Natural Resources 1996). Thus, techniques using collection records of single species are likely to give an overly generous impression of stability.

Our analyses focus on the ratio of 2 species in a single genus. In this data set, *P. maniculatus* was about equal to *P. leucopus* in the collections before 1920, and the descriptions of Kennicott (1857) confirm its abundance in prairie habitat in the 19th century. Why is the deer mouse less abundant than the white-footed mouse in recent museum depositions? Because museums have accepted large numbers of specimens of *Peromyscus* and *Microtus* in the last 30 years, the hypothesis that the collection only accepted specimens of rare or unusual species is rejected. The hypothesis that recent collectors actively sought *P. leucopus* cannot be excluded, but it seems unlikely. We did find that a substantial portion of the specimens labeled *P. maniculatus* were actually *P. leucopus* according to the criteria of Hoffmeister (1989), but the reclassified specimens were spread out over time so that the regression was not affected. The most parsimonious explanation of the reduced proportion of *P. maniculatus* and *M. ochrogaster* is the decline of their prairie habitat. While the total amount of all natural areas in this region has declined considerably, Illinois Natural Areas Inventory data (White 1978) indicate that prairies have suffered greater losses than woodlands. The greater loss of prairie than woodlands could have been by disproportionate loss of prairies compared with woodlands but also could be due to woody vegetation invasion of prairies.

While the Forest Preserve District of Cook County owns 8 quality oak forests designated as nature preserves totaling 1,344 ha, its 4 prairie nature preserves total only 78 ha (McFall and Karnes 1995). Altogether the prairie habitat totals only 122 ha in 7 Cook County Nature Preserves (McFall and Karnes 1995). With management these small areas can effectively preserve vegetation, but often lack animals, especially grassland birds. Grassland birds have declined more than other bird groups

(Herkert 1995; Peterjohn et al. 1995), so it is not surprising that prairie mammals also have experienced greater declines than woodland or generalist mammals.

The slopes of the lines estimating the decrease of all 4 proportions (total native prairie habitat, proportion of terrestrial habitat that is prairie, PPPero, and PPMicro) are similar with a range of -0.005 to -0.003. The *y*-intercepts, or proportion in 1840, of 3 of the 4 variables are similar (native prairie proportion, 0.76; proportion of terrestrial communities that are prairie, 0.81; PPPero, 0.85). These similarities strengthen the hypothesis that the loss of prairie mammals is a consequence of the loss of prairie habitat, but if *P. maniculatus* were completely dependent on native prairie, PPPero would probably be even lower than it is estimated to be.

Unlike *P. m. bairdii* which seems to be threatened by county-level extinction, Franklin's ground squirrel appears to be threatened on a broader scale. The species has not been collected in the 6-county Chicago region since 1971, and it is a listed species in the neighboring states of Indiana (endangered), Wisconsin (special concern), and Iowa (rare). No Franklin's ground squirrels were caught in the 8 most eastern Indiana counties of former range in a $>$5,000–trap-day study (Johnson and Choromanski-Norris 1992). In a recent central Illinois trapping survey, 12 sites with historical records of Franklin's ground squirrel occurrence were trapped, and in 1,032 trap-days, only 1 was caught (Hofmann 1999). Besides the loss of native prairie, a cause of its decline could include the increase in woody vegetation that is the apparent cause of the increased proportion of *P. leucopus*. Its listed status in neighboring states, lack of recent museum specimens, and lack of currently known viable populations in Illinois suggest that Franklin's ground squirrel should be on the Illinois list of endangered and threatened species. A more recent risk assessment utilizing published censuses and a telephone survey suggests Franklin's ground squirrel has become rare throughout the United States and vulnerable in Canada (Pergams 2001).

This paper highlights considerations in biodiversity planning by providing an example of how museum specimens may be used to evaluate status of habitat and species. Even though populations of all small mammals have declined in this urbanized region due to habitat consumption by human economic activity, prairie species have become especially rare and deserve special concern in biodiversity planning. Comparisons of collection records of $\geq$2 species with different habitat preferences provides an opportunity to measure environmental change (e.g., habitat, disease) that is otherwise confounded with collection effort in records of single species. Lastly, we have shown that the prairie deer mouse is likely to be at risk regionally, while Franklin's ground squirrel may be at risk on a broader scale.

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University of Alaska Museum, Santa Barbara Museum of Natural History, Natural History Museum of Berne (Switzerland), University of Hawaii Museum, and the Museum of Comparative Zoology at Harvard University. This work was funded by the University of Illinois at Chicago Campus Research Board, the Cook County Forest Preserve District in conjunction with The Nature Conservancy, and the Chicago Zoological Society. O. Pergams was supported by a United States Environmental Protection Agency Science to Achieve Results (STAR) Fellowship and a Grant-in-Aid of Research from the American Society of Mammalogists. O. Pergams thanks his wife, V. Morrow, for her loving support.

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Appendix I

Residences of specimens from the Chicago region used in analysis

Peromyscus.—American Museum of Natural History (1), Carnegie Museum of Natural His-

tory (6), Chicago Academy of Sciences (76), The Field Museum of Natural History (462), University of Illinois Museum of Natural History of the Illinois Natural History Survey (87), Illinois State Museum (31), Michigan State University (1), Museum of Comparative Zoology at Harvard (2), Museum of Vertebrate Zoology at University of California–Berkeley (6), National Museum of Natural History (7), Natural History Museum of Los Angeles County (11), Peabody Museum at Yale (1), University of Kansas (2), and University of Michigan (10).

Microtus.—Chicago Academy of Sciences (95), The Field Museum of Natural History (723), University of Illinois Museum of Natural History of the Illinois Natural History Survey (64).

Spermophilus franklinii.—American Museum of Natural History (6), Carnegie Museum of Natural History (1), Chicago Academy of Sciences (16), The Field Museum of Natural History (10), Illinois State Museum (4), Natural History Museum of Los Angeles County (2), University of Michigan Museum of Zoology (2), and Peabody Museum at Yale University (1).