# Island-specific Ecological Release of Small Mammals in Lake Michigan and Potential Consequences for Ground-nesting Birds: The Importance of American Beech *(Fagus grandifolia)* in Structuring Small-mammal Communities

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## Introduction

ISLAND AREA HAS THE POTENTIAL TO ALTER COMMUNITY AND ECOSYSTEM PROCESSES relative to the mainland (Wardle et al. 1997). Such differences include species composition (MacArthur and Wilson 1967), demographics (Adler and Levins 1994), and niche shifts (Crowell 1983). A suite of characteristics associated with island populations of rodents has been reported and collectively given the name "island syndrome" (Adler and Levins 1994). Island-related changes in density, morphology, and behavior are thought to result from the smaller area relative to the mainland, and the isolation of the island from the mainland. Observed changes in the structure of island populations of small mammals are thought to result from ecological release from interspecific competitors and predators found on the mainland but not on the islands (Adler and Levins 1994). Additionally, potential for dispersal is often limited on islands.

Studies examining the island syndrome have primarily focused on small mammals. Many small mammals are habitat generalists, with large demographic and ecological plasticity (Adler 1996). This allows relatively rapid changes to their ecology once introduced onto an island. In addition, other island taxa may be indirectly affected by island-related changes in small-mammal demography. For example, if ecological release on islands results in higher densities of small mammals relative to the mainland, island populations of ground-nesting songbirds may face unusually high nest depredation rates. Nest depredation accounts for approximately 80% of all nest failures for open-cup nesting passerines and has the potential to shape patterns of habitat selection, coexistence, and the evolution of life-history traits of birds (Martin 1988, 1993).

Ground and shrub-nesting birds in temperate deciduous forests are exposed to a variety of bird and mammalian predators (Schmidt et al. 2001), with *Peromyscus* spp. being documented as common nest predators (e.g., Guillory 1987; Maxson and Oring 1978). For example, nest failure of dark-eyed juncos *(Junco hyemalis* L.*)* in Virginia was positively correlated with deer mouse density, suggesting that mice influence the reproductive success of this

species (Flaspohler et al. 2000; Ketterson et al. 1996). This suggests that ground- and shrub-nesting birds breeding on islands may face unusually high nest depredation rates compared with the mainland where densities of predators are often higher.

Artificial nests are commonly used to compare relative rates of nest depredation among different habitats (Major and Kendal 1996). Although artificial nests are of limited use when estimating absolute rates of depredation on natural nests (e.g., Wilson et al. 1998), they have proven to be useful in estimating relative rates of depredation (Villard and Pärt 2004). By considering relative rates, the effect of over- or underestimation of absolute rates stemming from the use of artificial nests may be minimized. Additionally, the ability to manipulate the abundances and distribution of artificial nests allows a high degree of control, especially when natural nests are rare or difficult to find (Wilson et al. 1998).

Sleeping Bear Dunes National Lakeshore is located in the northwestern part of the lower peninsula of Michigan. It consists of North Manitou Island and South Manitou Island, with areas of approximately 33 sq km and 20 sq km, respectively, and approximately 290 sq km on the mainland. The forests at the national lakeshore are classified as northern hardwoods, although the species composition varies among the islands and the mainland. Vegetation analysis on the two islands shows distinctive differences in species composition, especially in trees over 10 cm diameter at breast height. The forests on South Manitou are composed of 10% American beech and 47% sugar maple *(Acer saccharum* Marsh.*)*, while North Manitou is 33% American beech and 46% sugar maple (P.M. Hurley, unpublished data). Understory vegetation structure also differs, with South Manitou having a higher level of herbaceous cover and North Manitou having a higher level of seedling and sapling cover.

We tested the null hypotheses that (1) there are no differences in the abundance of small mammals between the two Manitou islands in northern Lake Michigan and the mainland; and that (2) there are no differences in rates of artificial nest depredation on the islands compared with the mainland.

## Methods

Zebra finch *(Taeniopygia guttata* Vieillot)* eggs were used to simulate veery *(Catharus fuscescens* Stephens)* eggs. The veery was selected because it is a common ground-nesting bird on the islands and mainland. Zebra finch eggs (~16.9x12.8 mm) are smaller than veery eggs (~22.9x16.9 mm; Moskoff 1995), but readily obtainable commercial eggs were more similar to veery eggs than other species that have commonly been used in artificial nest studies (e.g., Japanese quail, *Coturnix japonica* Temminck & Schlegel). Real eggs were used in addition to the artificial eggs to mimic olfactory cues that may be associated with natural nests. Real eggs were left unwashed and kept in a refrigerator until they were placed in the artificial nests. Artificial nests constructed of dried grass were obtained from a craft distributor (Nicole Quality Value, Mount Laurel, N.J.). These nests were approximately 10 cm in diameter, 5 cm deep, and were similar in size to natural veery nests. Artificial eggs were made using gray Plasticine (Hobbycraft Canada, Concord, Ontario), which was rolled by hand into a shape and dimension similar to veery eggs. A small paper clip was then inserted into each egg, and the eggs were wired into the artificial nests to

minimize their loss. Each nest consisted of one artificial and one zebra finch egg. Latex gloves were worn at all times when the eggs and nests were being handled to minimize human scent contamination.

Four artificial nest grids each were located within the national lakeshore in beech–maple forests on the mainland, South Manitou, and North Manitou. Grids were a minimum of 1 km apart and were chosen using a digital vegetation cover type map such that all grids were located in similar forests. Each 200x200-m grid consisted of five parallel transects onto which nests were placed at 50-m intervals for a total of 25 nests per grid. The 50-m spacing was intended to limit the probability of a single predator depredating more than one nest. Artificial nest points were located at each interval using two random numbers: the first determined the distance from the transect (1–10 m in 1-m increments), and the second determined the direction from the transect (90° right or left of the transect). Artificial nests were placed in the leaf litter to simulate natural nests. No additional attempt was made to conceal the nests so as to avoid any bias associated with differences in concealment. Flagging was used to assist in relocation of the nests, but it was at least 25 m from any nest to minimize visual cues that predators may have associated with the nests. Simple sketches were also made for each nest to assist in relocation.

The veery breeding season lasts from approximately 1 June through 15 July. Artificial nest trials were performed on the mainland between 29 May and 10 June, on South Manitou between 31 May and 12 June, and on North Manitou between 15 June and 27 June. Logistical constraints precluded performing the artificial nest study at the same time at all three locations.

Nests were monitored after 6 days and again after 12 days, approximating the incubation period for the veery. A higher frequency of nest monitoring was avoided to reduce predator attraction to nests resulting from the presence of humans.

Successful nests were those that did not experience a depredation event after the 12-day exposure period. Artificial nests were considered depredated if the Plasticine egg had marks on it or if the zebra finch egg was destroyed or missing. Depredated nests were removed to avoid potential bias from predators learning the location of and returning to previously depredated nests. Plasticine eggs from depredated nests were collected and teeth marks were compared with teeth from a collection of small mammal skulls to determine the species responsible for the depredation event. All nests were removed after the 12-day monitoring period.

Small-mammal trapping was carried out between 20–24 June on the mainland, 25–29 June on South Manitou, and 1–4 July on North Manitou. One trapping grid was centered in each artificial nest plot. Small-mammal trapping occurred after the artificial nest study had been completed between 29 May and 27 June. Each trapping grid was 90x90 m, with traps spaced at 15-m intervals to create a 7x7 grid of traps. One 9x9x23-cm Sherman live trap (H.B. Sherman Traps, Tallahassee, Fla.) was placed at each trap station for a total of 49 Sherman traps per grid. These traps were covered with an insulating/waterproofing material and contained a single piece of cotton (i.e., nesting material) to minimize animal mortality in the traps. Additionally, nine Havahart traps (152 cm x 152 cm x 406 mm) were placed evenly on each grid to sample larger mammals. Flagging was

placed near each trap to aid relocation. Traps were baited with a mixture of peanut butter and rolled oats. Baited traps were used because the goal of this study was to establish an index of small-mammal abundance for each site rather than absolute density.

All animals were handled according to the American Society of Mammalogists guidelines (Animal Care and Use Committee 1998). Traps were checked daily in the early morning, and all captured animals were identified to the species level, weighed, and assigned to an age class. Age class was determined by pelage color for mice *(Peromyscus* spp.; Whitaker 1997) and weight for eastern chipmunks *(Tamias striatus)*, and animals were designated as juvenile, sub-adult, or adult. Captured animals were also ear tagged with serially numbered Size 1 Monel ear tags (National Band and Tag Company, Newport, Ky.) for future identification. We compared the age classes of *Peromyscus* spp. and eastern chipmunks captured at each location to determine whether the age structure of small-mammal populations differed over the two-week period.

Comparisons of artificial nest depredation rates were made among the islands and the mainland using CAPTURE (Otis et al. 1978). Population estimates were calculated for both mice and eastern chipmunks using NOREMARK (White 1996). *Peromyscus* spp. were pooled due to difficulty in distinguishing the deer mouse *(Peromyscus maniculatus* Wagner*)* from the white-footed mouse *(Peromyscus leucopus* Rafinesque*)* in the field and the ecological similarity of the two species (Schnurr et al. 2002). Lincoln-Peterson population estimates of small mammals on the islands and the mainland were compared using multiple analysis of variance (MANOVA) (SAS Institute Inc. 1989). Age structure of *Peromyscus* spp. was compared among the three locations using hierarchical log-linear analysis in SPSS (SPSS Inc. 1998). Planned orthogonal contrasts (mainland vs. South Manitou and North Manitou; North Manitou vs. South Manitou) were then made using a G-test. Age-class comparisons of chipmunks between North and South Manitou were made using a Student's t-test (SAS Institute Inc. 1989). For all analyses, an alpha of <0.10 was considered statistically significant.

## Results

After 6 days, the mean number of nests depredated out of 25 on North Manitou was significantly higher than on either South Manitou or the mainland ($F_{CALC}=10.87$, $p=0.004$, df=11; Figure 1). Since nearly all of the nests on North Manitou were depredated after six days, analysis of nest success on this island was limited to the 6-day depredation rate. After 12 days, nearly all nests on the mainland and South Manitou were depredated, and depredation rates were not statistically significantly different between these two locations ($t_{stat}=0.37$, $p=0.72$, df=6; Figure 1).

Examination of depredated Plasticine eggs indicated that *Peromyscus* spp. were responsible for most of the nest depredation on both islands and the mainland (Table 1). Eastern chipmunks, gray squirrels *(Sciurus carolinensis* Gmelin*)*, and northern flying squirrels *(Glaucomys sabrinus* Show*)* accounted for a small proportion of artificial nest depredation events on both islands, but these species were not responsible for any known nest depredation events on the mainland and were never captured there. The mainland did have higher rates

Figure 1. Mean number of artificial nests depredated after 6 and 12 days on the mainland, North Manitou Island, and South Manitou Island at Sleeping Bear Dunes National Lakeshore, Michigan. Error bars represent one standard error. Each location consisted of four independent grids, each consisting of 25 artificial nests. On Days 6 and 12, bars with the same letter are not significantly different (*p*>0.05). On North Manitou Island, nearly all nest were depredated after 6 days. Therefore, no Day 12 analysis was available for this island.
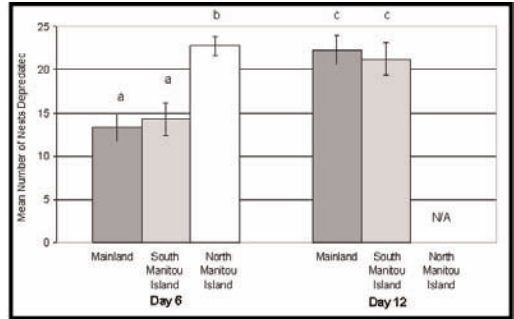


|  | Peromyscus spp. | Eastern chipmunk | Raccoon | White-tailed deer | Unidentified Avian | Unknown |
|---|---|---|---|---|---|---|
| Mainland | 77% | 0.0% | 13% | 1% | 0% | 9% |
| S. Manitou | 88% | 2% | 0% | 0% | 0% | 10% |
| N. Manitou | 87% | 3% | 2% | 0% | 2% | 6% |

Table 1. Percentage of artificial nests depredated by different predators on the mainland, North Manitou Island, and South Manitou Island at Sleeping Bear Dunes National Lakeshore, Michigan. Each of these three locations consisted of four independent grids, each consisting of 25 artificial nests.

of raccoon *(Procyon lotor* L.*)* depredation, and all three locations had nests that were removed completely and assigned to an "unknown" category. Other predators such as white-tailed deer *(Odocoileus virginianus* Boddaert*)* and birds played relatively minor roles as artificial nest predators.

Indices of population sizes of *Peromyscus* spp. among the mainland, South Manitou, and North Manitou were not significantly different ($F_{CALC}$=0.83, *p*=0.25, df=11; Figure 2). Variation in capture success within each location was high and may have reduced the chances of detecting differences in population sizes among the three locations. Eastern chipmunk population estimates among the mainland, South Manitou, and North Manitou (0, 5.9 ± 3.1, and 11.3 ± 3.1, respectively) were significantly different ($F_{CALC}$=4.94, *p*=0.03, df=11; Figure 3). No chipmunks were captured on the mainland

during the trapping period, despite occasional sightings on the mainland.

Hierarchical log-linear analysis of *Peromyscus* spp. captured at each location revealed that age classes were more evenly distributed on the mainland than either of the two islands, where most of the individuals captured were adults (*p*=0.004). Planned contrasts of this data suggest that the mainland contained proportionately more non-adult mice than either of the islands ($G_{CALC}$=6.71; *p*<0.01) and that the two islands did not differ from one another ($G_{CALC}$=0.09; *p*>0.05). However, no statistically significant differences were seen in the age distribution as inferred from mean body weights of eastern chipmunks on South Manitou versus North Manitou.

Other captured species included southern red-backed voles *(Clethrionomys gapperi* Vigors*)*, gray squirrels, northern flying squirrels, and northern short-tailed

Figure 2. Mean estimated population sizes of mice *(Peromyscus* spp.) on the mainland, North Manitou Island, and South Manitou Island at Sleeping Bear Dunes National Lakeshore, Michigan. Each of these three locations consisted of four independent grids, each with a 7x7 grid of small-mammal trap stations. Error bars represent one standard error. At each location, bars with the same letter are not significantly different ($p$>0.05).
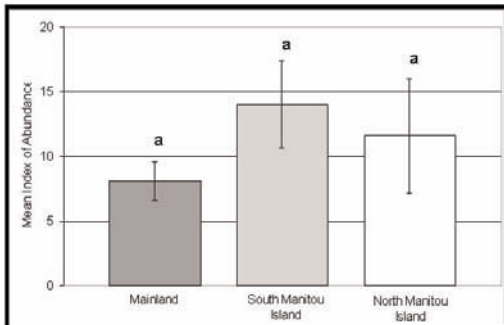


Figure 3. Mean estimated population sizes of eastern chipmunks *(Tamias striatus)* on the mainland, North Manitou Island, and South Manitou Island at Sleeping Bear Dunes National Lakeshore, Michigan. Each of these three locations consisted of four independent grids, each with a 7x7 grid of small-mammal trap stations. Error bars represent one standard error. At each location, bars with the same letter are not significantly different ($p$>0.05).
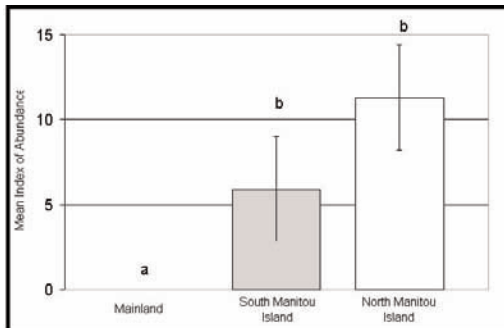
shrews *(Blarina brevicauda* Say*)*, but these species were not caught in sufficient numbers to estimate population sizes. In addition, these species were never implicated as nest predators.

## Discussion

Many authors have questioned the use of artificial nests to estimate rates of nest depredation of natural bird nests. Factors such as human scent contamination (Donalty and Henke 2001); lack of adult scent and incubating activity; presence of eggs but not nestlings; differences in camouflage; lack of adult defense; differences in the size, color, or odor of eggs (Wilson et al. 1998); attraction of different suites of predators; differences in the location of nests (Zanette 2002); and the ability of some predators to learn to search for artificial nests arranged in a regular pattern (e.g., a grid; Willebrand and Marcstrom 1988) may result in dis-

crepancies between artificial and natural nest depredation. However, there appears to be a growing consensus that artificial nests are valuable for measuring nest depredation at local scales (Roper 1992) and detecting trends in relative reproductive success in birds (Wilson et al. 1998; Villard and Pärt 2004).

Our study suggests that some interesting community processes are occurring at Sleeping Bear Dunes National Lakeshore. Small-mammal communities differ among the Manitou islands and the mainland. However, the differences that we identified were only partly consistent with predictions of ecological release of small mammals on both islands. On North Manitou, eastern chipmunk population densities were higher than on either South Manitou or the mainland. North Manitou Island also had significantly higher depredation rates on artificial nests after six days than either South Mani-

tou or the mainland. In terms of small-mammal populations and artificial nest depredation rates, South Manitou resembled the mainland more than it did North Manitou. We had predicted similar patterns between the islands and differences between the islands and the mainland. If ecological release of small mammals occurred on both islands, it was either manifesting itself in different ways or was obscured by other phenomena that are simultaneously acting on small mammals on the islands. For example, island-specific population fluctuations may have obscured the effects of the island syndrome. In some cases, it has been suggested that intraspecific competition resulting from elevated population densities may increase and thereby overcome any effects resulting from lack of interspecific competition on islands (Crowell 1983). However, on the Manitou islands, population densities of the major artificial nest predator (*Peromyscus* spp.) did not appear to be elevated, and although population densities of eastern chipmunks on North Manitou were higher than on the mainland, they did not appear to be the dominant nest predator.

Historically, South Manitou has lacked a population of white-tailed deer. In contrast, North Manitou went through several decades (1940s–1980s) of extremely high deer densities while it was a private game reserve with supplemental winter food provided (Case and McCullough 1987). These populations have persisted, and deer are still present on North Manitou. Mainland deer densities have historically been intermediate between the densities on the two islands. American beech is approximately three times more abundant on North Manitou than on South Manitou (D. Flaspohler, unpublished data). We hypothesize that the preference of deer for sugar maple

over American beech (Case and McCullough 1987) has favored beech recruitment on North Manitou relative to South Manitou and led to the greater dominance of beech on North Manitou compared with South Manitou or the nearby mainland. This beech dominance and associated greater abundance of beech seed may be supporting the higher relative densities of chipmunks that were observed on North Manitou, potentially increasing competition with mice for food resources. This, in turn may explain the higher level of artificial nest depredation by mice on North Manitou relative to the mainland and South Manitou. This study suggests a potentially important role of American beech in structuring forest communities, although other possible mechanisms behind these observations may exist. Clearly, further work would be valuable in beginning to uncover the mechanisms observed at the national lakeshore.

In addition to the competitive relationships discussed above, it is possible that mammals on the islands have a later reproductive season than those on the mainland because of the close proximity to Lake Michigan. If this is accurate, population estimates of *Peromyscus* spp. on the mainland may have been somewhat inflated relative to those on the islands, because the breeding season had apparently already started on the mainland (as evidenced by the relatively even distribution of age classes on the mainland). Relatively few juvenile and sub-adults were captured on the islands, and it is likely that they had not experienced the same reproductive output when they were sampled. However, both islands appeared to be fairly similar in the distribution of age classes, both for *Peromyscus* spp. and for eastern chipmunks. Later sampling of mammals on the islands

may have provided a more detailed representation of relative population sizes, particularly between the mainland and the islands.

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