Dispersal of White-footed Mice, *Peromyscus leucopus*, in Low-density Island and Mainland Populations

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Demographic attributes of dispersing White-Footed Mice, *Peromyscus leucopus*, on Muskeget Island, Massachusetts, and the adjacent mainland were compared. Densities of both populations were low throughout the five years of study. The number of dispersers was positively correlated with the number of residents in both populations, but the rate of dispersal was not related to the density of the resident populations. Dispersers of both sexes on Muskeget reached sexual maturity at a lower weight than residents. On the mainland, male dispersers reached sexual maturity at a lower weight than residents, whereas female dispersers reached sexual maturity at a greater weight than residents. A greater number of young females dispersed on Muskeget than expected, whereas more young males dispersed than expected on the mainland. Adult males may have been important in limiting recruitment on the mainland but not on Muskeget Island. We hypothesize that there is a relationship between the roles of males and females in limiting recruitment and the relative positions of *Peromyscus* populations on the r and K selection continuum.

Key Words: demography, dispersal, Massachusetts, *Peromyscus leucopus*, r and K selection, White-footed Mouse.

Dispersal has been found to be important in the demography of small mammal populations (reviewed by Lidicker 1975; Gaines and McClenaghan 1980; Tamarin 1980). Experimental studies of dispersal have been conducted on a number of species of small mammals including members of the genera *Clethrionomys* (Kozakiewicz 1976), *Geomys* (Williams and Cameron 1984), *Microtus* (Myers and Krebs 1971; Krebs et al. 1976; Tamarin 1977a; Krebs et al. 1978; Beacham 1979; Gaines, Baker and Vivas, 1979; Keith and Tamarin 1981; Baird and Birney 1982a, 1982b; Gaines and Johnson 1984), *Peromyscus* (Garten and Smith 1974; Sullivan 1977; Fairbairn 1977a, 1978a; Nadeau et al. 1981; King 1983), *Reithrodontomys* (Joule and Cameron 1975), *Sigmodon* (Joule and Cameron 1975; Stafford and Stout 1983), and *Synaptomys* (Gaines, Vivas and Baker 1979). Studies of island populations generally show that dispersal is reduced in these populations (Mazurkiewicz and Rajska 1975; Sullivan 1977; Tamarin 1977a).

Nadeau et al. (1981) analyzed dispersal of White-footed Mice, *Peromyscus leucopus*, in relation to population structure on Muskeget Island, Massachusetts, and concluded that males did not limit recruitment or determine population structure, in contrast to most other population studies of *Peromyscus*. Adler and Tamarin (1984) compared demographic and reproductive attributes of the White-footed Mouse on Muskeget Island and on the adjacent mainland and found important differences in several attributes. If dispersal is closely linked to demography, then we would expect to find important differences in the process of dispersal on Muskeget Island and the mainland. In this study, we compared demographic attributes of dispersing White-footed Mice on Muskeget Island and the adjacent mainland.

Materials and Methods

Muskeget Island is a small sandy island located 32 km south of Cape Cod, Massachusetts. The habitat of Muskeget is dominated by Beach Grass (*Ammophila breviligulata*) and Poison Ivy (*Rhus radicans*).

Two 0.8 ha control grids (grids A and B of Tamarin, 1977b) were established to monitor residents on Muskeget. Both grids consisted of a 10 × 10 matrix of trap stations with 7.6 m between stations. One Longworth live-trap baited with oats and supplied with cotton for bedding occupied each station. Traps were set for two consecutive nights and checked the following mornings. Trapping was conducted approximately monthly.

Captured mice were ear-tagged with fingerling fish tags, sexed, and weighed. Reproductive data were recorded and consisted of position of the testes (scrotal or abdominal) in males and vaginal patency and nipple size in females. Obvious pregnancies were detected by palpation. Mice were released at their point of capture after data were recorded.

A 0.8 ha experimental grid (grid E of Tamarin 1977a) was established 30.4 m from grid B to collect dispersers. Mice captured during the first trapping period were considered residents and permanently removed. All mice colonizing the grid after the initial removal period were considered dispersers and were permanently removed during every subsequent trapping period. Data were gathered on dispersers in a manner similar to residents, but dispersers were sacrificed and returned to the laboratory for autopsy.

A similar trapping design was followed on the mainland. The control grids (grids D and F of Tamarin 1977b) were located in Barnstable and Plymouth, Massachusetts, respectively. Both grids were dominated by the grass *Poa pratensis*. The removal grid (grid G of Tamarin 1977a) was located 30.4 m away from grid F. Grid G was rectangular. The first 8 lines nearest grid F were 8 stations long and the last 4 lines were 9 stations long.

Trapping on Muskeget began in May 1972 and was continued until August 1977. Trapping at Barnstable began in June 1972 and was terminated in January 1976 and trapping began at Plymouth in October 1972 and continued until July 1977.

We used the age classes of Adler and Tamarin (1984). Because of the small numbers of juveniles and subadults captured, we combined these two age classes together as young.

Results

Dispersal and Density

Density changes on Muskeget were described by Nadeau et al. (1981) and Adler and Tamarin (1984). Density changes on the mainland were described by Adler and Tamarin (1984). Density changes in both populations were characterized by an annual cycle in numbers with densities highest in autumn and winter and lowest in spring.

To determine the relation of dispersal to density, we calculated the total number of mice caught per 100 trapnights in each season (winter, spring, summer, and autumn) on the two control grids combined and the removal grid at each site (Figures 1 and 2). Total trapnights varied from 600 to 1200 per season on the two control grids combined at each site and from 200 to 600 per season on the removal grids at each site.

To determine if density was an important determinant of dispersal, we regressed number of dispersers on number of residents calculated in each three-month period (N = 20 periods on the mainland and 21 periods on Muskeget). Both regressions were statistically significant. On the mainland, 37.9% of the variation in the number of dispersers was explained by the density on the control grids ($F = 10.98$, $p < 0.005$), whereas 74.0% of the variation in dispersal was explained by density of residents on Muskeget ($F = 53.94$, $p < 0.001$).

To further analyze the relation of dispersal to density, we calculated recovery ratios (Krebs et al. 1976) for each season. The recovery ratio is a dispersal rate and is defined as (the number of dispersers at time t)/(the number of residents at time t). The overall recov-

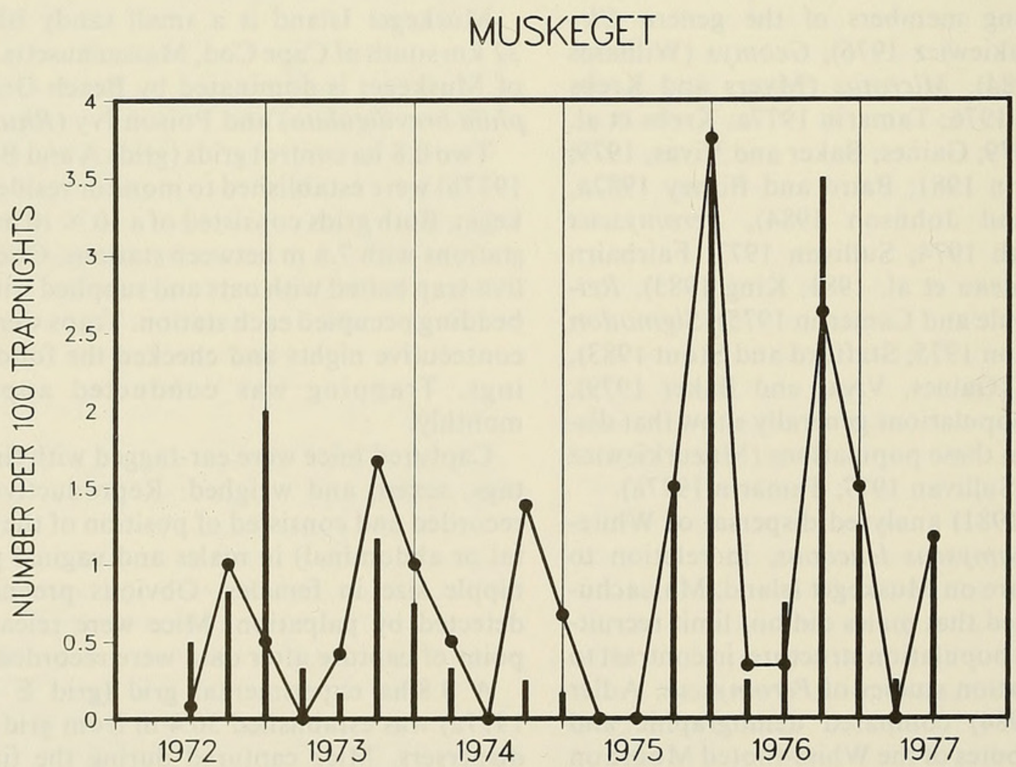

FIGURE 1. Seasonal density estimates of resident and dispersing White-footed Mice on Muskeget Island.
The solid dots connected by lines indicate the number of residents.
The solid vertical bars represent the number of dispersers.
Vertical lines separate years.

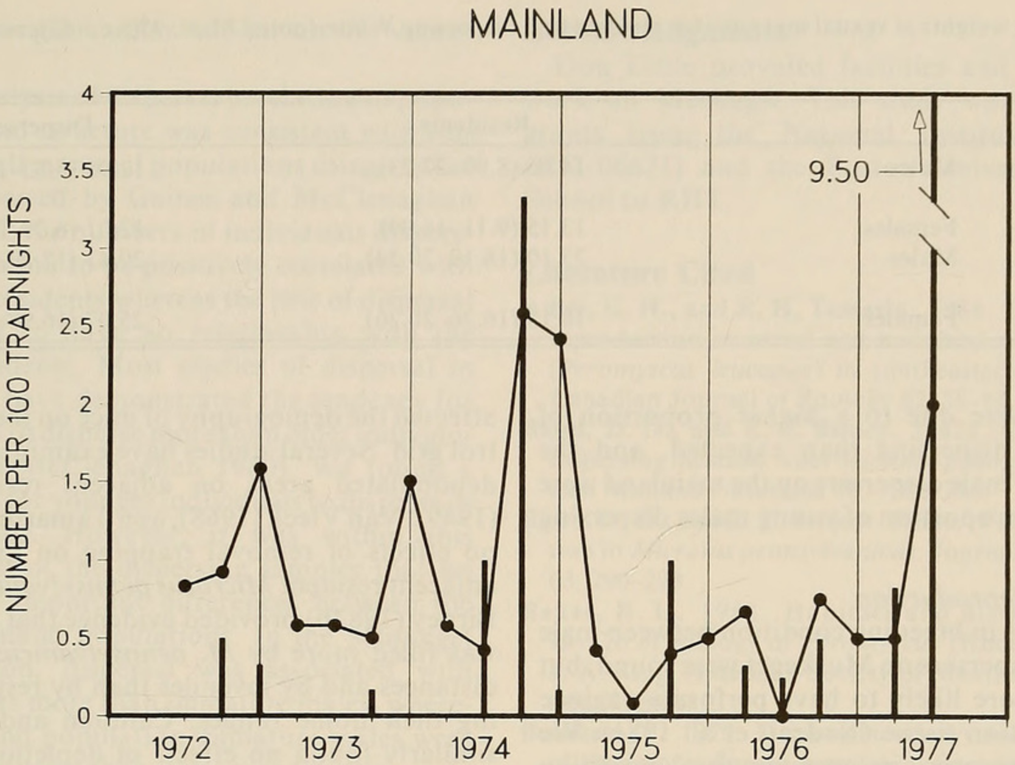

FIGURE 2. Seasonal density estimates of resident and dispersing White-footed Mice on the mainland. See legend for Figure 1.

ery ratio was 1.22 on the mainland and 1.01 on Muskeget. The last period on the mainland was characterized by an unusually high number of dispersers (9.50 per 100 trapnights). With this last period on the mainland omitted, the overall recovery ratio was only 0.66. To determine if dispersal rate was dependent upon density, we regressed dispersal rate on density. Dispersal rate was density-independent in both populations ($F = 0.27$, $p > 0.25$ for the Muskeget population; $F = 1.97$, $p > 0.10$ for the mainland population).

Thus, dispersal was correlated with density in both populations, dispersal rate was nearly twice as high on Muskeget as on the mainland (with the one period characterized by the high number of dispersers on the mainland omitted), and the rate of dispersal was density-independent in both populations.

Dispersal and Population Structure

Nadeau et al. (1981) found no differences in sex ratios (males/female) between dispersers and residents. Similarly, we found no differences in sex ratios between dispersers and residents in the mainland population (resident sex ratio = 0.81, N = 136; disperser sex ratio = 1.34, N = 68; $\chi^2 = 2.83$, $p >= 0.05$).

We compared the numbers of adult and young residents and dispersers in both populations (Tables 1 and 2). In the mainland population, more young males dispersed than expected, and on Muskeget more young females dispersed than expected.

Female dispersers weighed less than residents, but dispersing males were similar in weight to resident males on Muskeget (Nadeau et al. 1981). We found dispersing males to be lighter in weight than resident males in the mainland population ($F = 5.10$, $p < 0.025$), but we found no differences between females. Thus, the lower weights of female dispersers

TABLE 1. Numbers of adult and young residents and dispersers in the mainland population of White-footed Mice.

		Adults	Young	Chi-square
Males	Residents	54	7	10.37*
	Dispersers	24	15	
Females	Residents	47	28	1.79
	Dispersers	14	15	

*$p < 0.005$

TABLE 2. Numbers of adult and young residents and dispersers in the Muskeget Island population of White-footed Mice.

		Adults	Young	Chi-square
Males	Residents	67	26	0.53
	Dispersers	32	9	
Females	Residents	37	14	4.85*
	Dispersers	15	16	

*$p < 0.05$

TABLE 3. Median weights at sexual maturity for resident and dispersing White-footed Mice. 95% confidence intervals are in parentheses.

		Residents	Dispersers
Muskeget	Males	14.06 (8.90–22.23)	12.96 (5.83–28.78)
	Females	13.15 (9.11–18.99)	12.01 (6.09–21.56)
Mainland	Males	23.10 (18.19–29.34)	20.43 (17.29–24.13)
	Females	18.15 (16.26–20.26)	25.07 (16.98–37.00)

on Muskeget were due to a higher proportion of young females dispersing than expected, and the lower weights of male dispersers on the mainland were due to a higher proportion of young males dispersing than expected.

Dispersal and Reproduction

No differences in breeding condition between male residents and dispersers on Muskeget were found, but females were more likely to have perforate vaginae and small lactation tissue (Nadeau et al. 1981). We found no differences in reproductive condition between residents and dispersers in either males or females on the mainland.

We calculated median weights at sexual maturity for male and female residents and dispersers in the two study populations using the probit technique of Leslie et al. (1945) (Table 3). Only data from breeding seasons were used, and these data were pooled over the entire study period. Obviously pregnant females were excluded from the analysis.

Male and female dispersers on Muskeget had slightly lower median weights at sexual maturity than residents. On the mainland, male dispersers had lower median weights than residents whereas female dispersers had higher median weights at sexual maturity than residents.

Discussion

The White-footed Mouse is widely distributed in the eastern United States and southern Canada. Although it is primarily a woodland species (Baker 1968), Adler and Tamarin (1984) reported resident populations of White-footed Mice in grasslands of Muskeget Island and adjacent mainland Massachusetts. This situation has allowed a comparative study of dispersal in this species in similar habitats.

The removal grid has been widely employed in monitoring dispersal (reviewed by Gaines and McClenaghan 1980). However, mice defined as dispersers in our study may simply have been neighboring mice expanding or shifting their home ranges into a depopulated area. If this explanation were true, then the removal of mice on the experimental grid may have affected the demography of mice on the adjacent control grid. Several studies have examined the effects of depopulated areas on adjacent residents. Hayne (1949), Van Vleck (1968), and Tamarin (1977a) found no effects of removal trapping on home ranges of adjacent resident *Microtus pennsylvanicus*. Baird and Birney (1982b) provided evidence that vacant habitat was filled more by *M. pennsylvanicus* moving long distances and by juveniles than by residents expanding their home ranges. Calhoun and Webb (1953) similarly found no effects of depletion trapping on home ranges of *Blarina, Sorex, Peromyscus,* and *Clethrionomys*. Stickel (1946) found a movement of resident *Peromyscus* into depopulated areas. Tamarin (1977a) found a statistically significant movement of *Microtus breweri* toward a removal grid. Mares et al. (1980) also found a movement of nearby *Tamias striatus* into a depopulated area. However, most migrating *Tamias* individuals were juveniles which presumably left due to social pressure from adults. Thus, vacant areas had apparently little effect on movements of adult *Tamias* residents.

Three separate lines of evidence suggest that the removal grids had little effect on the demography of *Peromyscus* on the control grids in our study. First, 13% and 18% of the mice recovered from the mainland and Muskeget removal grids, respectively, were expected to have been tagged on the control grids (Tamarin 1977a). However, only 6% of the mice on the mainland grid F moved to grid G, and only 13% of the mice on Muskeget grid B moved to grid E.

Second, if mice were shifting their home ranges in response to the vacant removal area, then mice on the control grid should simply have moved short distances to the removal grid. Although sample sizes were insufficient in our study to provide a proper analysis, data from two other *Peromyscus* populations in southeastern Massachusetts indicated that distance was not important in the movement of mice onto removal grids, whereas habitat characteristics were important (Adler ms.). Adler (ms.) hypothesized that these *Peromyscus* individuals left the control grids in response to social pressure or resource limitation and then sought similar habitat on the vacant removal grids.

Third, our analysis of dispersal in relation to population density and structure was consistent with studies of other small mammal populations using similar techniques (reviewed by Gaines and McClenaghan 1980). In general, the numbers of individuals dispersing have been found to be positively correlated with the numbers of residents whereas the rate of dispersal has been found to have no relationship with the numbers of residents. Most studies of dispersal in small mammals have demonstrated the tendency for younger animals to disperse more than older individuals (Gaines and McClenaghan 1980). We found a similar tendency for younger individuals to disperse in both populations. However, it was within this younger segment of the dispersing samples that we found the most important differences between the island and mainland populations. In the Muskeget Island population, dispersal was associated with immature females more than immature males, whereas in the mainland population immature males were more likely to disperse than immature females.

Fairbairn (1978a) hypothesized that the preponderance of dispersing *Peromyscus* did so due to social pressures from residents or to low resource levels. Since young individuals dominated the disperser samples in both of our study populations, it is likely that dispersers were social subordinates.

Most studies of *Peromyscus* populations showed that males limited recruitment and determined population structure (Healey 1967; Petticrew and Sadlier 1974; Fairbairn 1977a, 1978a, 1978b). However, three studies suggested that males had little effect in determining population structure (Metzgar 1971; Harland et al. 1979; Nadeau et al. 1981). Our results indicated that the mainland population was more similar to the majority of *Peromyscus* populations studied since young males were overrepresented in the disperser sample. Thus, adult male *Peromyscus* on the mainland may have led to the dispersal of subordinate males (Howard 1949; Sadlier 1965; Healey 1967; Fordham 1971; Garten and Smith 1974; Petticrew and Sadlier 1974; Fairbairn 1977a, 1977b, 1978a, 1978b; Mihok 1979).

Adler and Tamarin (1984) noted differences in demography and reproduction between the Muskeget Island and mainland populations which indicated the mainland population was more K-selected. Nadeau et al. (1981) hypothesized that the roles of males and females in limiting recruitment and densities in *Peromyscus* populations may differ. We hypothesize that there is a relationship between the role of males and females in limiting recruitment and the relative positions of *Peromyscus* populations along the r and K selection continuum.

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