DEMOGRAPHY AND DISPERSAL IN ISLAND AND MAINLAND
POPULATIONS OF THE DEER MOUSE,
Peromyscus maniculatus

by

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Abstract

If dispersal is reduced on islands, then the demography of island populations of deer mice should be different from that of mainland populations. Areas of 1.1 ha were periodically cleared of mice on Samuel Island (206 ha) and Saturna Island (3102 ha) in the Gulf Islands of southwestern British Columbia. A similar experiment was conducted on the mainland at Maple Ridge, B.C. The average density of mice per hectare on Saturna (43.5) was twice that on Samuel Island (22.0) and nearly two and one-half times higher than that on the mainland (18.7). The reproductive rate, as measured by length of breeding season, number of successful pregnancies, proportion of breeding animals, and number of recruits surviving to breed, was much higher on Samuel Island than on either Saturna or the mainland. Survival was lowest on Samuel Island, with little difference between the mainland and Saturna Island. Mice on Samuel Island grew more than five times faster than mainland animals, and Saturna growth rates were double those on the mainland. Island adult males showed very few aggressive tendencies in laboratory behaviour tests compared with the seasonal changes in aggression reported in the literature for mainland deer mice. Dispersal (or colonization) rate was reduced on the two islands compared with that on the mainland. Recruitment of young animals occurred throughout the breeding season on the islands but was delayed until the end of breeding on the mainland. There was little difference in the demographic attributes of control populations when compared with those of colonist populations on either the

mainland or the two islands. These results indicate that seasonal changes in aggressiveness of the adult population may be sufficient but not necessary to determine breeding density and seasonal changes in survival of juvenile deer mice. A more intensive study is required, but regulatory processes in populations of Peromyscus maniculatus may be different on islands and perhaps should not be generalized over different geographic areas.

TABLE OF CONTENTS

Abstract	i
TABLE OF CONTENTS	iii
LIST OF FIGURES	iv
LIST OF TABLES	v
ACKNOWLEDGEMENTS	vii
INTRODUCTION	1
DESCRIPTION OF STUDY AREAS	3
MATERIALS AND METHODS	5
RESULTS	8
Trappability	8
Population Density and Recruitment	9
Population Density and Dispersal	11
Reproduction	16
Reproduction and Dispersal	17
Mortality	19
Survival and Dispersal	23
Growth	23
Growth Rates and Dispersal	25
Sex Ratios and Dispersal	27
Introduction Experiments	28
Behaviour	29
DISCUSSION	30
SUMMARY	41
FIGURES	42
TABLES	64
LITERATURE CITED	79

LIST OF FIGURES

Figure 1.	Location of study areas.	42
Figure 2.	Aerial photograph of study areas.	44
Figure 3.	Population density on mainland control and experimental grids.	46
Figure 4.	Population density on Samuel Island control and experimental grids.	48
Figure 5.	Population density on Saturna Island control and experimental grids.	50
Figure 6.	Survival in the three control populations. ...	52
Figure 7.	Percentage of animals sexually mature in various weight classes.	54
Figure 8.	Body weight distributions for control populations.	56
Figure 9.	Growth rates for control and experimental populations.	58
Figure 10.	Median body weight at sexual maturity for control and experimental populations.	60
Figure 11.	Schematic representation of seasonal changes in populations of deer mice.	62

LIST OF TABLES

Table 1.	Trappability estimates for control populations.	64
Table 2.	Adult and juvenile recruitment in the breeding season.	65
Table 3.	Control population density and colonization data.	66
Table 4.	Comparison of observed range length in control and experimental populations.	67
Table 5.	Proportion of mice in breeding condition in control populations.	68
Table 6.	Proportion of mice in breeding condition on control and experimental areas during removal weeks. . .	69
Table 7.	Comparison of proportion of mice in breeding condition for control and pulse populations.	70
Table 8.	Survival rates for control populations.	71
Table 9.	Indices of early juvenile survival and reproductive data for control populations.	72
Table 10.	Comparison of survival rates for control and experimental populations.	73
Table 11.	Age classes of animals.	74
Table 12.	Growth rates for animals in control populations.	74
Table 13.	Sex ratios in control and experimental populations.	75
Table 14.	Results of introduction experiments.	76
Table 15.	Results of behaviour tests for island mice. . .	77

Table 16. Summary of demography and dispersal in island and mainland populations of deer mice.	78
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INTRODUCTION

The role of dispersal in the demography of small mammals has received much attention in recent years. The relation of dispersal to population regulation has been experimentally studied in Microtus spp. by Myers and Krebs (1971) and Krebs et al (1976) and in Peromyscus spp. by Garten and Smith (1974) and Fairbairn (1976). Islands provide natural laboratories where hypotheses concerning the possible role of dispersal in regulating numbers may be experimentally tested. The Gulf Islands off the coast of southern British Columbia and the adjacent mainland provide areas for studying dispersal in populations of deer mice, Peromyscus maniculatus.

Populations of deer mice in southern B.C. fluctuate seasonally with low spring breeding densities and high densities through the fall and winter. During the breeding season, recruitment is low, with few juveniles surviving to trappable age. It is currently thought that seasonal changes in the survival of juvenile mice are determined by seasonal changes in the aggressiveness of the adult population (Sadleir 1965; Healey 1967; Fordham 1971; Petticrew and Sadleir 1974; and Fairbairn 1976).

Previous work involving Peromyscus maniculatus on the Gulf Islands has suggested that island mice are poorer dispersers and have a lower variance in population size relative to mainland mice (Redfield 1976). If dispersal is reduced on the islands, how does the demography of island populations of deer mice compare with that of mainland populations? One technique for

determining these effects is to produce a vacant area in good deer mouse habitat and then to measure the rate of colonization of the vacant habitat. The trapped-out area has been adopted as a technique for studying dispersal. Resident deer mice are periodically removed from an area, which dispersing animals then colonize. This study was designed to: 1) compare demographic attributes and seasonal changes in island and mainland populations of deer mice, 2) test the hypothesis that rates of dispersal are lower on islands than on the mainland, 3) compare demographic attributes of dispersing animals with those of residents in control populations.

DESCRIPTION OF STUDY AREAS

This research was done on Samuel Island and Saturna Island in the Gulf Islands and on the mainland in the U.B.C. Research Forest at Maple Ridge, B.C. (Figure 1). Samuel Island is 206 ha (510 acres) in area with a fairly dense cover of successional forest composed of Douglas fir, western hemlock, western red cedar, and grand fir. Salal dominates the understory. Saturna Island is 3102 ha (7680 acres) in area and exhibits various successional stages following logging. The area used in this study was virgin Douglas fir forest with western hemlock and western red cedar of secondary importance. Salal was the most prevalent species in the understory.

Two very small islands were used as areas for introductions of island and mainland populations of mice. King Islet is 0.16 ha (0.4 acre) in area with a vegetation cover of shrubs and herbs, and is located between Samuel Island and Saturna Island. Reef Island is 1.6 ha (4.0 acres) in area, and has predominantly shrub and herb cover with some trees (Douglas fir and Madrone). It is located east of Samuel Island. An aerial photograph of these four island study areas is given in Figure 2.

All these islands are located in the Coastal Douglas fir zone of Krajina's (1965) biogeoclimatic classification. The climate is mild with little temperature fluctuation and a fairly low amount of precipitation, most of which occurs in the winter season.

The mainland study area is covered by second growth forest dominated by western hemlock and western red cedar with some

Douglas fir. Ground cover vegetation is sparse. The Research Forest is located in the Coastal Western Hemlock zone (Krajina 1965) with greater temperature fluctuations and amounts of precipitation than on the islands.

MATERIALS AND METHODS

From March 1974 to May 1975, three control and three pulse removal grids were live-trapped every two weeks with Longworth live-traps. All grids were 1.1 hectares in area. One control grid and one pulse removal grid were located on each of the islands as well as the mainland. Large island (Saturna) and mainland grids had 49 trap stations (7x7), and small island (Samuel) grids had 50 trap stations (5x10). All trap stations were located at 15.2-m intervals marked by flagging tape and string or stakes. One live-trap was placed within a 2-m radius of each station. Traps were baited with peanut butter and Purina lab chow, and Terylene batting was supplied as bedding. Traps were set on day 1, checked on days 2 and 3, and then locked open between trapping periods. During November 1974 to March 1975, traps were set for one night only and checked the following day. Snow interrupted trapping from Dec. 28 to Jan. 24 on the islands and from Dec. 28 to Mar. 12 on the mainland.

All deer mice captured were weighed on Pesola spring balances, sexed and ear-tagged with serially numbered fingerling fish tags. The duration of the breeding season was noted by palpation of male testes and the condition of vaginal openings and mammaries of the females. Mice were released immediately after processing on the control grids. The pulse removal grids were trapped on a 12-week cycle of 2 trapping periods of complete removal followed by 4 trapping periods of mark and release trapping. This allowed mice to colonize the removal area and establish a resident population between removal

periods. Distances between control and pulse removal grids were as follows: 600 m on mainland, 1500 m on Saturna island, and 600 m on Samuel island.

Population parameters were determined by enumeration techniques to avoid the statistical assumptions of random sampling. Hilborn et al. (1976) have demonstrated by a simulation model that enumeration techniques provide sufficiently accurate estimates for a trapping design in which 80% or more of the animals are caught each sampling time. Age classes of animals were determined by body weight.

For the introduction experiments, approximately equal numbers of island and mainland mice were introduced onto King Islet and Reef Island on May 10, 1974. These islands were not previously inhabited by mice (Redfield 1976). The areas were trapped July 29-31 for two nights with small Sherman live-traps, and the number of surviving animals as well as new offspring were recorded. All mice were removed from King Islet at this time, and the experiment was repeated with much higher densities of island and mainland mice. This island was trapped again on Oct. 18-20 for two nights, and the number of surviving animals and offspring was recorded. For these experiments, mainland mice were collected from the removal grid at U.B.C. Research Forest and from trap-lines set on the U.B.C. Endowment Lands. Island mice were from the Samuel and Saturna Island pulse removal grids.

Behaviour tests in the lab were conducted on males in reproductive condition from Samuel and Saturna Island control populations. No tests were done on mainland animals. Fourteen

animals were collected from each island in July, 1975 and tested after a 3- to 5-day lab adjustment period. Tests were conducted in a neutral arena in the dark under a 100-watt red bulb. Each of seven pairs of animals was allowed a 5-minute habituation period with behaviours (aggressive and cohesive) recorded at 5-second intervals over an interaction period of ten minutes. A brief description of these behaviours is given in Table 15.

RESULTS

In the appropriate figures and tables, each of the grids is designated by a letter in the following manner: mainland control - A and pulse removal - B; Samuel Island control - C and pulse removal - D; Saturna Island control - E and pulse removal - F.

Two age classes of deer mice have been used by Sadleir (1965), Britton (1966), Healey (1967), and Fordham (1971): juveniles and adults. I refer to these two age classes of adults and juveniles (animals in juvenile and subadult age classes pooled together) throughout the results and discussion. Juveniles are considered to be young animals recruited during the breeding season.

The data analysis in this study is complicated by the same animals being captured in several sampling periods. Consequently, chi-square analyses have been utilized for data in which the samples are not completely independent. Examples are the proportion of animals in breeding condition, survival rates, and sex ratios. For this reason, the tests may not be statistically valid but are used as an indication of the degree of difference between sets of data. Chi-square analyses have been used to test for differences in various demographic attributes between control populations, between control and removal animals, and between control and pulse populations.

Trappability

The demographic analysis of these island and mainland populations is based on the assumption that most of the individuals in a given population are captured. Maximum

trappability has been defined by Krebs et al. (1976) as follows:

trappability =

No. actually caught at time i / No. known to be present at time i

Minimum unweighted trappability is a less biased estimate since it eliminates first and last captures, and provides only one value for each individual regardless of how long it lives. Both of these estimates for the three control populations are given in Table 1. As expected, maximum trappability is higher and is always above 79%. Minimum unweighted trappability is above 70% except for males on Saturna Island. There is no difference in trappability of males and females on Samuel Island. Mainland females and Saturna males have the lowest trappabilities, which in the latter case is probably associated with the higher density on this area.

Population Density and Recruitment

The population changes for the three study areas were different and will be discussed separately. The density of the control population on the mainland is shown in Figure 3. Density was low before breeding commenced and subsequently increased owing to an influx of new adult animals 3-4 weeks after the breeding season had begun. Numbers averaged about seventeen through the breeding season with very little recruitment. The number of juvenile recruits averaged 1.0 male and no females per trapping week of breeding season. In September, breeding ceased and there was the typical increase in

juvenile recruitment into the population. More males were recruited into the population than females at this time. Numbers increased through October to a peak of 32 animals and then stabilized for the duration of the winter. In early spring, density again decreased at the start of the next breeding season.

Population changes on the Samuel Island control grid are illustrated in Figure 4. Breeding began in early April and numbers declined until late June, when recruitment of juveniles increased the density. Recruitment was continuous through the breeding season with peak density reached in mid-November. Juvenile recruits averaged 2.9 males and 2.2 females per trapping week of breeding season. More males were recruited than females during the last few weeks of the breeding season, otherwise there was very little difference in males and females throughout the study. Numbers were stable through the winter with little recruitment compared with that in the breeding season. There was approximately one and one-half times the number of animals at the start of the 1975 breeding season compared with the previous year. The non-breeding season was four months long on this small island compared with nine months duration on the mainland.

The control population for Saturna Island is shown in Figure 5. Breeding began in early May with a slight decline in density until recruitment of juveniles started in July. Juvenile recruits averaged 3.1 males and 1.8 females per trapping week of breeding season. Numbers peaked at the end of breeding in September and remained high through the winter. The

non-breeding season was approximately six months duration on this large island. The 1975 breeding season began in late March with juveniles recruited into the population during April and May. Numbers declined at the start of both breeding seasons until recruitment of young animals increased the density. The average density of mice per hectare on Saturna (43.5) throughout the study is twice that on Samuel Island (22.0) and nearly two and one-half times higher than that on the mainland (18.7).

Population Density and Dispersal

Results for the pulse removal grid on the mainland are shown in Figure 3. There are four total removal periods of one month duration each. The first, second, and last removals are followed by a two-month interval. The third removal is followed by a four-month interval when snow interrupted trapping for several weeks. Colonization and then establishment of a resident population comparable to the pre-removal density as well as that of the control grid occurred within two weeks in the first three pulse periods. The response after the fourth pulse removal is somewhat similar, but was hampered by skunk disturbance on the trapping area during the second removal week and the first week of colonization. Also, this pulse removal occurred at the same time as numbers on the control grid were declining. A total of 95 animals was removed from this grid during the study.

Results for the Samuel Island pulse removal grid are shown in Figure 4. The dispersal (colonization) rate of animals onto this grid was slow following the first and second removal weeks of the first pulse. Numbers did not reach the pre-removal or

control densities until eight weeks later. The other pulse periods showed more immediate responses following each removal. Density due to colonization stabilized at pre-removal and control levels 10 weeks after the second removal, six weeks after the third removal, and eight weeks following the fourth removal. The final pulse period showed a higher dispersal (colonization) rate compared with the first pulse but again recovery to a stable density was not completed. The first and last pulse removals occurred approximately one year apart. Colonization during the first two weeks of the final pulse was greater than that of the first. This probably reflects the higher control density (one and one-half times) and later start of the breeding season in 1975 compared with declining numbers after the start of the breeding season in 1974. A total of 168 mice was removed from this grid during the study.

Data from the Saturna Island pulse removal grid are shown in Figure 5. Dispersal (colonization) rate was slow during the recovery following the first removal period. Density did not stabilize to the level of pre-removal or control populations until eight weeks after the removal. The second pulse had a much more rapid rate of dispersal within the first two weeks of colonization. Numbers stabilized at the pre-removal level about four weeks into the pulse and reached a density comparable to that of the control after ten weeks. The third pulse showed a similar initial rate of colonization and after four weeks stabilized below pre-removal and control densities. The fourth pulse removal was interrupted by snow, with the result that not all animals were removed. Subsequent colonization near to the

pre-removal level occurred within two weeks, and after ten weeks was still below that of the control. The final pulse removal took place in the spring of 1975 approximately one year after the first. The removal periods and initial colonization were very similar. The breeding season was in progress each year and control and pre-removal densities were comparable. Thus, this final pulse can be considered a sequential replicate of the first pulse period. A total of 262 animals was removed from this grid during the study.

A comparison of recruitment during removal weeks in the breeding season for control and pulse removal grids is shown in Table 2. On the mainland, very few adults or juveniles entered the control population compared with the numbers that were recruited onto the removal grid. However, on Samuel Island, during the removal weeks of the second and third pulses, similar numbers of male juveniles but not females entered the control and experimental populations. For total numbers, this is significantly different from that on the mainland ($p < .05$). In both pulses, more adults colonized the removal area than were recruited into the control population and these animals were predominantly males. Saturna Island showed a greater number of juveniles colonizing the removal area compared with recruits into the control population. When compared with the mainland, this difference is not statistically significant ($p = .06$), but is of biological significance because of its similarity to Samuel Island. There is little difference between grids with respect to adults.

In this study, dispersal (or colonization) rate can be

measured in three ways: number of new mice colonizing pulse removal grid during the two weeks following each total removal, recovery ratio and recruitment index (Krebs et al. 1976). Observed range length is used as a possible check on these three techniques.

Recovery ratio=

No. mice colonizing removal grid at time i / Population size on control grid or pulse removal grid at time i

Relative recruitment index=

No. mice colonizing removal grid at time i / No. new recruits tagged on control grid at i

The first three measures for the experimental populations are presented in Table 3. The recovery ratio may be used as a measure of the resiliency of the control population as well as the experimental population which has colonized and resided on the pulse removal grid. The average recovery ratio, expressed as a percentage, for the control populations is highest on the mainland (pulses 1,2, and 3) at 95.8%. Both islands have a much lower resiliency: Samuel Island with 57.3% and Saturna (pulses 1,2,3, and 5) at 36.9%. There is no overlap in 95% confidence limits between data for the mainland and Saturna Island which suggests a significant difference in this measure of dispersal rate. The average recovery ratio for the pulse populations similarly is highest on the mainland at 97.4%, with Samuel Island (59.9%) and Saturna (50.7%) being substantially lower.

There is virtually no overlap in confidence limits between data for the mainland and Samuel Island and very little overlap between the mainland and Saturna.

The relative recruitment index averaged 8.25 on the mainland. This means for every new mouse captured on the control area during these removal weeks, approximately 8 animals colonized the pulse removal grid. The islands both had much lower average indices of recruitment, with Samuel Island at 3.44 and Saturna at 3.30.

Since islands have restricted land area, observed range length should be a fairly good index of the movement of mice and, consequently, the ability to disperse. Table 4 summarizes observed range lengths for males and females on the control and pulse removal grids of each study area. Only mice with more than one capture were used for these calculations. Movement of males on the mainland control is not significantly different from that on either island control. However, Saturna males have a significantly smaller range length than do those on Samuel. Control and experimental males show no difference on either island. Males from the experimental population on the mainland show a significantly larger average range length than do their control counterparts. This is biologically significant, since it is evident that those animals colonizing the pulse removal grid on the mainland have a higher rate of dispersal than similar mice on either island. Movement of females is not significantly different for control and experimental populations between islands (Table 4). Mainland females have larger range lengths than females on the islands, and this result again is

statistically and biologically significant. There is no difference in female movement between mainland control and experimental grids.

In summary, the number of mice moving into depopulated areas as measured by two recovery ratios and recruitment index is much greater than on either island. This is further supported by movement of animals, as measured by observed range length, which is significantly greater on the mainland than on the islands.

Reproduction

The best variable to use for determining the breeding activity of a population is probably the percentage of lactating females (Krebs et al. 1969). This parameter underestimates the start of active breeding by the length of the gestation period, which is about three weeks. Percentage of females with medium to large nipples and percentage of males with scrotal testes have been used to determine the length of breeding season for my three control populations.

On the mainland, the 1974 breeding season extended from mid-June to early September (ca. 12 weeks). On Samuel Island the duration of breeding was from mid-April to mid-December (ca. 34 weeks) with some animals in reproductive condition up to late January 1975. The 1975 breeding season began in early May at both of these study areas. Breeding commenced in mid-May 1974 on Saturna Island and extended to mid-September (ca. 18 weeks). There was sporadic breeding in early October. The 1975 breeding season began in mid-March and continued through to the end of the study in late May.

Table 5 gives three measures of breeding performance for the control populations during June to August of the 1974 breeding season. A significantly higher percentage of adult males was in breeding condition on Samuel Island compared with Saturna. Although not statistically significant, the mainland population also had a higher percentage of males with scrotal testes compared with Saturna. There was no difference in percentage of adult females with a perforate vagina. Island comparisons for juveniles for these two measures of breeding intensity were not significantly different. Mainland animals in this age class could not be compared with those on the islands because of low sample size. Samuel Island had a significantly higher percentage of adult females lactating compared with Saturna and a 10% increment over the mainland. An estimate of litter size for Saturna Island mice was obtained from laboratory animals and averaged 3.38 ($N=32$, range 2 to 5). This figure may be compared with mainland litter sizes determined by other workers (Sheppe 1963; Sadleir 1974).

Reproduction and Dispersal

A comparison of breeding intensity for all removal weeks for control and pulse removal grids is given in Table 6. There was no difference in breeding intensity between control and dispersing males of either age class on any of the study areas. Adult and juvenile females showed no difference in breeding intensity as measured by lactation. Of the adult females colonizing the removal grid on Samuel Island, the percentage with a perforate vagina was significantly higher compared with the control population ($p<.05$). Similarly, adult female

colonizers on Saturna Island also had a higher percentage ($p=.06$) for this measure of breeding intensity. However, this may not be biologically significant because condition of the vaginal opening shows much variability (Sadleir 1974), and both island experimental grids have low sample size relative to those for control populations. Percentage of lactating females is probably more reliable for determining the breeding activity of a population but it is impossible to get a rapid response in the lactation measure to a sudden removal situation.

The reproductive performance of the pulse populations after colonization is given in Table 7. There was a significantly higher percentage of adult males with scrotal testes on the Saturna experimental grid during the first and second pulses as well as the total. The second pulse population on Samuel Island also had more reproductive adult males than did the control. Mainland adult males showed no difference in reproductive performance between control and pulse populations. Similarly, where sample size allowed statistical comparison, juveniles did not vary significantly in control and pulse populations for either scrotal testes or perforate vagina. Percentage of adult females with perforate vagina also follows this pattern. There is no significant variation in percentage of lactating females on the mainland or Samuel Island, but the trend from the totals is a lower number of females with medium to large nipples among the pulse populations compared with the control. The Saturna Island adult females show a higher percentage of lactation in the first pulse population, a difference which may be biologically significant.

To summarize, males and females colonizing the experimental grids following each removal week did not differ significantly in reproductive condition from control animals for any of the study areas. However, in the subsequent pulse populations, breeding intensity was significantly higher in adult males on Saturna Island and during the second pulse on Samuel Island. It was significantly lower for lactating adult females during the second pulse on Saturna. Mainland control and experimental populations showed similar reproductive attributes.

Mortality

Mortality in this study is represented by disappearance from the trappable population, and so includes emigration. Temporal changes in survival rates are measured by direct enumeration, and include survival in the trappable population and early juvenile survival.

Minimum survival rates for all males and females in the three control populations in this study are presented in Figure 6. The average survival rates are given for breeding (summer) and non-breeding (winter) seasons in Table 8. These average rates are summed over a season with an individual mouse being tallied each time it is trapped.

On the mainland, male survival showed a large drop at the start of the breeding season, and was lowest in July 1974 and again in April 1975. Females survived poorly before the breeding season started, and then remained fairly stable up to May of the following year, when survival slipped below 50%. Survival of males was lower in the summer compared with winter ($p=.07$) and female survival was the same in each season. Male

survival was lower than that of females in summer (not statistically significant) with no difference in the winter. Both males and females showed a steady increase in survival towards the end of and after the breeding season. On Samuel Island, both sexes (particularly males) had very poor survival during most of the breeding season. It improved toward the end of breeding and remained high through the winter. Average survival was significantly higher ($p < .01$) in winter for both males and females. Male survival was lower than that of females in both seasons but the difference is not statistically significant. Saturna Island males had lowest survival during summer 1974, increased towards the end of breeding and remained high through the winter (difference significant at $p < .01$). Female survival was high throughout the study, with little difference between seasons. It may be biologically significant that survival of females was greater than that of males during the breeding season.

Table 8 presents comparisons of minimum survival rates for different seasons and age classes for males and females in the three control populations. Low sample size for winter 1974 populations at the start of the study did not permit statistical comparisons. During summer 1974, adult males and juvenile females on Saturna Island had significantly better survival than on Samuel Island. Mainland adults and Saturna juvenile males also had higher survival than those of Samuel, but this is not significant. Totals for the two age classes show significantly higher survival on Saturna and the mainland for both males and females. This trend continued through winter 1974-75 for males,

but there are no differences in total female survival. Age class distinctions for deer mice can be determined only during the breeding season. Total survival through the study for all males and females was significantly lower on Samuel Island compared with Saturna. This was also true for total mainland males but not for females. Total survival on the mainland and Saturna was very similar for both sexes.

Early juvenile survival may be measured by an index relating recruitment of young into the trappable population to the number of possibly lactating females (Krebs 1966):

index=

No. small mice in week t / No. females with medium to large nipples caught in week $t-4$

Small mice were defined as those less than 17 g on the mainland, 19 g on Samuel Island, and 21 g on Saturna Island. Different gram weights were used in accordance with the discussion of variation in body weights and growth rates. Table 9 gives the mean indices for the three control populations during the breeding season and up to the end of recruitment of young. In the breeding season, early juvenile survival on Samuel Island was ten times higher than that of the mainland and one and one-half times higher than that of Saturna Island. Early juvenile survival was also much better on Saturna than on the mainland. With the addition of recruitment after the breeding season, the two island indices changed very little. However, the mainland increased to 0.66 and this late recruitment was reflected in the

increase in total density in the fall for the control population (Figure 3).

The number of successful pregnancies, litter size, and expected and observed number of juveniles which were recruited into each control population during the breeding season are listed in Table 9. Samuel Island had the highest number of successful pregnancies as well as observed number of juveniles entering the population. Saturna Island had slightly more successful pregnancies than the mainland and a much higher recruitment of juveniles. Of animals which were recruited into control populations up to one month before the end of breeding, 46% males and 50% females survived at least two weeks and 29% males and 47% females survived and bred on Samuel Island (Table 9). On Saturna, 60% males and 75% females survived, but no males and only 3 of 8 females survived and bred. The mainland had 2 of 3 males surviving after being caught two weeks before the end of breeding.

In summary, total male survival for all control populations and total female survival on Samuel Island were significantly lower in summer compared with winter. Samuel adult males and juvenile males and females survived very poorly relative to Saturna Island. Adult females showed little difference. Winter survival rates were poorest on Samuel Island, and showed very little variation between Saturna and the mainland. Total survival through the study was lowest on Samuel, with little difference between the mainland and Saturna Island. Early juvenile survival was highest on Samuel Island, followed by Saturna and then the mainland.

Survival and Dispersal

To determine if dispersing (colonizing) animals survived better than those in control populations, survival rates should be compared between each two-month pulse period and a similar time period on the control. Table 10 presents this comparison for males and females on the three study areas. There was no difference in survival between residents and colonizing mice for either sex on the mainland. The poor survival of animals in pulse no. 3 for both males and females was probably due to low sample size on the experimental grid. Total survival was similar for males and somewhat lower for pulse females compared with the control. Saturna Island likewise showed no difference between control and experimental animals. Survival was slightly higher in male populations of the first and last pulses and lower in pulse no. 1 for females, but total survival was similar for both sexes. On Samuel Island, males survived significantly better on the experimental grid during the first and third pulses as well as overall. Female survival was significantly higher for the first three pulse populations compared with control survival. The fourth pulse showed a lower but still high survival rate relative to control.

To summarize, there was little variation in survival between control and colonist populations on Saturna Island or the mainland. However, both male and female deer mice on Samuel Island survived better in most pulse populations relative to control animals.

Growth

Growth rates may be used as a further index of conditions

within populations of Peromyscus maniculatus. The aspects of growth to be considered are sexual maturity and body weight, growth rate regressed on body weight, and body weight distributions.

Age at sexual maturity is a useful demographic variable for determining the age classes of deer mice. Owing to the lack of a better criterion, body weight must be used as an index of age. The percentage of sexually mature animals in a series of weight classes may be used to determine the weight limitations for juveniles, subadults, and adults. Figure 7 presents this comparison for males and females in the control and pulse populations during the breeding season. Males and females and control and pulse populations did not differ significantly with respect to these histograms. My age classes assume juveniles are seldom, if ever, sexually mature; individuals of which less than 50% are mature in the upper weight class are called subadults; and adults must have at least 50% of mice sexually mature in the lowest weight class. Using these criteria, I estimated the weight limits for age classes from Figure 7 and these limits are listed in Table 11.

To show that the differing weights of age classes are equivalent among study areas (e. g. is a 17-g adult mouse on the mainland equivalent in age to a 21-g adult mouse on Saturna Island?), there must be variation in growth rates. Since growth rate is dependent on body weight, regressions for these variables may be compared between study areas. Table 12 summarizes analysis of covariance of growth rate regressed on body weight of animals less than 20 g from June to October.

Males and females had similar growth rates and have been combined for the three control populations. Samuel Island mice have a growth rate 5.6 times that of mainland mice and 2.8 times that of Saturna mice, which in turn grow twice as fast as mainland animals. Thus, the island animals do grow much faster than their mainland counterparts, and so the age classes used throughout this paper are reasonably accurate.

Body weight distributions for breeding (summer) and non-breeding (winter) seasons for males in control populations are shown in Figure 8. Body weights were higher in the summer compared with winter for the mainland and Samuel Island. There is little difference on Saturna, which may reflect the lower intensity of breeding on the larger island. Both islands have animals weighing up to 32 g. During breeding, there are very few mainland adults above 24 g in weight and none above 26 g. Samuel Island has the highest number of mice in juvenile and subadult weight classes. During the winter, most mainland males are in one weight category (16-17 g), and on Samuel the majority weigh 20-23 g. Saturna males are evenly spread over 5 weight classes (20-30 g).

Growth Rates and Dispersal

The growth rates of individuals comprising the pulse populations on removal areas should be equal to or better than those on control grids. Mean growth rates (adjusted to 13-g animals on the mainland and Samuel Island and 15 g on Saturna Island) and 95% confidence limits of males for control and pulse populations are shown in Figure 9. None of the individual means is significantly different because of the broad confidence

intervals. Growth was slightly better on the mainland pulse removal grid during the first, third, and fourth pulses. On Samuel and Saturna Islands, growth rates in pulse populations were less (except pulse no. 3 on Saturna) than for control animals. There is more variation in the female data, which are also presented in Figure 9. Experimental females on the mainland had slightly better growth during the first and third pulses, but a lower growth rate for the second pulse. There were insufficient data to plot an average value for the fourth pulse population. Saturna females showed slightly better growth in the experimental population relative to control for the first three pulses and then decreased considerably in the final pulse. Females were growing better in the first, second, and fourth pulses, but much poorer during the third pulse on Samuel Island. In general, growth of mainland animals remained fairly stable through time whereas the growth rates of Samuel Island animals decreased during the study, and those of Saturna decreased and then improved in the last pulse.

Age at sexual maturity is also a useful variable for determining if colonizing mice are maturing at the same age as control animals. The weight at sexual maturity for live-trapped mice was estimated in the same manner as described for voles by Krebs et al. (1976). Figure 10 presents these data for males and females during the period June to October 1974. The body weight of male deer mice at sexual maturity was the same for control and pulse populations on the mainland. However, island experimental males tended to mature at lighter weights than control animals, a difference that is significant on Saturna

Island but not on Samuel. Females on all study areas matured at slightly lower weights in pulse compared with control populations. From a comparison of male and female control animals it is apparent that mainland females matured at weights nearly 3 g heavier than males, but island mice showed very little difference.

In summary, animals on Samuel Island grew more than five times faster than mainland mice, and Saturna growth rates were double those on the mainland. This variation in growth substantiates age class distinctions showing Saturna adults 4 g heavier and Samuel adults 2 g heavier than their mainland counterparts. Mainland experimental males tended to have better growth than control animals, whereas island experimental males had slightly lower growth rates. In general, female growth on experimental areas was better than on controls, but there was some variation for specific pulse periods. Both sexes of island experimental animals and females on the mainland tended to mature at lighter weights compared with control populations.

Sex Ratios and Dispersal

The sex ratio of control areas has been estimated by tallying each animal every time it is captured and summing these data for the entire study and the four removal periods. This technique provides a weighted average sex ratio for control and colonizing populations. Both the mainland and Saturna control populations had a significantly higher ($p < .05$) proportion of males (0.58) compared with Samuel Island (0.50). Table 13 gives the sex ratios for control and colonizing populations of the three study areas. More males colonized the removal area than

females on Samuel Island, and this is significant for the total. The proportion of mainland males varied from one pulse to the next, but there was no difference in the total ratio. On Saturna, the proportion of males was less than the control in the first removal period, but there was a transition through the study to a higher proportion in the final removal. Since age class distinctions in P. maniculatus can only be made during the breeding season, there are insufficient data to determine a difference in sex ratio between juveniles from experimental and control areas and that of adults. Comparison of sex ratios of mice colonizing removal areas with those of new recruits on control areas showed no difference.

Introduction Experiments

To test for possible differences between island and mainland deer mice with respect to colonizing ability, behaviour, and survival, approximately equal numbers of animals were introduced to two small islands. The results of three introduction experiments are listed in Table 14. There were no significant differences (chi-square analyses) in relative success or survival of either island or mainland mice. It was not possible to identify untagged offspring as of either island or mainland origin. The total number of mice introduced onto Reef Island averaged 19.75 animals per acre and the number introduced in the second King Islet experiment equalled 167 per acre. At the end of these experiments the density on Reef Island increased to 21.5 per acre and King Islet was 120 animals per acre. It was hoped that these abnormally high densities might result in either mainland or island mice dominating owing

to a higher level of agonistic behaviour. However, no valid conclusions may be drawn from these experiments except that deer mice can survive for a short period of time, and at least some individuals reproduce at these very high densities.

Behaviour

This investigation into behaviour of island and mainland mice is preliminary and represents the behaviour of animals under laboratory conditions. Results of behaviour tests for Samuel and Saturna Islands are listed in Table 15. There appear to be very few aggressive tendencies in island mice. Samuel Island males had a much shorter latency period before first recorded behaviour and twice the number of interaction intervals compared with those of Saturna. This may reflect a lower level of general activity among the large island animals compared with those from Samuel. These results are not consistent with those of Sadleir (1965), Healey (1967), and Fairbairn (1976) who showed seasonal changes in aggressive behaviour of male adult deer mice.

DISCUSSION

In the experimental part of this study, deer mice were removed from areas for one month, followed by establishment of a resident population during the next two months. Consequently, it is possible to measure the rate of colonization onto the vacant area and monitor the performance of animals which become established. Individuals which appear on the vacant area were classed as 'dispersers,' and are probably surplus animals driven out of adjacent populations. This experiment was designed to study the colonizing ability of dispersers at 3-month intervals throughout the year. It is unlikely that all the mice which colonized the pulse removal grids were animals which would have been dispersing out of undisturbed populations. However, I think it is safe to assume that this sample would contain a higher proportion of dispersing individuals than would resident samples from control areas. The work of Stickel (1946) and Fairbairn (1976) with deer mice from continuous removal grids tends to support this assumption. Several other assumptions for experimental designs involving removal of animals from an area have been discussed by Krebs et al. (1976).

Control and removal grids were separated by a distance beyond which there could be any effect on population processes in the control area due to removal of mice from the experimental area. This precluded catching tagged individuals which dispersed from the control, but was necessary owing to the wide ranging activity of deer mice (Stickel 1968). Therefore, I am assuming my distant control populations give an adequate

representation of events occurring around the removal area.

A second assumption is that most resident and colonizing mice are removed during the two removal weeks between pulse periods. *P. maniculatus* is very trappable and readily enters unfamiliar traps. Thus, the wave of colonizing mice following a month removal are assumed to be surplus animals dispersing onto a vacant habitat. It is also possible that colonizing mice are just wandering individuals which shift homesites every few weeks or months. I do not have the behavioural data to determine whether colonizing mice are socially subordinate animals or are wanderers moving through the population.

A pulse removal was used in this study instead of a continuous removal because it allows capture of animals colonizing a vacant habitat and then monitors the demographic performance in the following two months. It should also be noted that a continuous removal on Samuel Island may have had adverse effects on the control population by acting as a sink for this small island (510 acres).

Populations of deer mice have been experimentally studied on the mainland of southwestern British Columbia by Sadleir (1965), Healey (1967), Fordham (1971), Petticrew and Sadleir (1974), and Fairbairn (1976). Seasonal changes in these populations of *P. maniculatus* are summarized in Figure 11. The results from my study at the U.B.C. Research Forest at Maple Ridge tend to agree with most aspects of the demographic changes associated with this annual cycle of numbers in deer mice. There is an increase rather than a decline at the onset of breeding. Overwinter mortality may have reduced the population

to the point that too few animals are present to exploit the habitat efficiently and immigrants move in from adjacent areas. As discussed by Healey (1967) and Fairbairn (1976), the spring reorganization may not necessarily be a decline in numbers. It should involve increased immigration and emigration, and density may decrease, increase, or show no net change. Fairbairn (1976) also suggests that a decrease in density of males at this time is a response to mortality of early breeding females. However, the first lactating females on my mainland control grid did not suffer heavy mortality. This may be due to delayed start in breeding (mid-June) in 1974 such that energy requirements (food and weather conditions) were favourable for successful reproduction. Petticrew and Sadleir (1974) working in this same forest found the start of breeding to be much earlier in 1969 (February) and in 1970 (April).

The populations on Samuel Island and Saturna Island showed some differences from the model population presented in Figure 11. There are two basic differences in demography, apart from density, between the islands and mainland.

Firstly, there is a lower rate of dispersal on the islands as measured by observed range length and by three indices derived from the number of new mice colonizing the pulse removal grid. This is most pronounced during the spring reorganization, when male density on Saturna (1974 and 1975) and density of males and females on Samuel Island is declining. There does not appear to be a surplus of animals on either island at this time. This may be an indication that animals are not being driven out of the resident population by social pressure, but are dying on

the grid. This is further supported by the colonization of experimental areas being more rapid in removal weeks during the rest of the year when a surplus or spill-over of animals must be available from the breeding season.

Although rapid colonization of my mainland pulse removal grid occurred before breeding, Fairbairn (1976) has shown by two pulse removal experiments on U.B.C. Endowment Lands that animals moving around in undisturbed areas during the spring reorganization would rapidly colonize a depopulated area. Her control populations were declining at this time, which is similar to what was happening on my island control areas. Thus, these dispersing mainland mice represent surplus animals which were presumably driven out of the resident population.

Breeding was continuous after starting in April on Samuel Island and in May on Saturna Island (1974). There was no pulse of early breeding before the main breeding season began on the islands compared with that recorded by Fairbairn (1976) on the U.B.C. Endowment Lands. An exception may be the 1975 breeding season on Saturna Island which began in March and appeared to taper off in mid-May when the study ended. There was heavy mortality of early breeding females on Samuel Island, and survival of males was also very poor at this time. These results are consistent with the poor survival of early breeding females and subsequent decline in density of males recorded by Fairbairn (1976). However, on Saturna Island, the first lactating females survived very well in both 1974 and 1975.

Secondly, recruitment of juveniles occurs throughout the breeding season with peak densities reached before the end of

breeding. This recruitment into control populations on the islands was verified by the experimental areas. The equivalent number of juveniles colonizing the pulse removal grid and entering the control population during removal weeks provided this support. On the mainland, as expected, animals colonizing the pulse removal during removal weeks and the first two weeks of the second pulse period were primarily juveniles. There was virtually no recruitment into the control population at this time. This result contradicts that of Fairbairn (1976), who had poor dispersal of juveniles, but high dispersal of adults onto removal areas. It is possible my experiment of periodically removing animals during breeding may not be comparable to a continuous removal experiment. However, the number of juveniles versus adults dispersing onto a removal grid is a function of age classes based on body weight. Fairbairn (1976) used a juvenile weight class of under 15 g whereas I used 17 g. Since juvenile animals may be growing rapidly at this time of year, the high number of adults colonizing a depopulated area may include a fair proportion of mice which are actually young recruits. If this is the case, then animals not able to enter a resident population disperse in an attempt to find an open space to settle in. This was suggested by Healey (1967) as a mechanism for getting rid of the excess of recruits during years of low mortality.

Preliminary results from behaviour tests indicate that island adult males in breeding condition show virtually no aggressive behaviour. This is further supported by Halpin's work (pers. comm.) which showed no evidence of aggressive

behaviour between island adults and juveniles in the neutral arena. On the mainland, Sadleir (1965), Healey (1967), and Fairbairn (1976) have found an increase in adult male aggression during the breeding season. Sadleir (1965) and Healey (1967) have also established that adult males in mainland populations inhibit growth and survival of juveniles at this time.

A behavioural difference between island and mainland mice may explain reduced dispersal on the islands, particularly during the spring reorganization. If there is little aggressive interaction or social pressure forcing animals out of the population on the islands in order to establish a breeding density, then colonization of depopulated areas will be slow. The ability of juveniles to reach trappable age and even enter the population may also be a result of this lack of aggressive behaviour.

The reproductive rate as measured by length of breeding season, number of successful pregnancies, percentage of breeding animals, and number of recruits surviving to breed is much higher on Samuel Island than on either Saturna or the mainland. This high reproductive rate is responsible for the high recruitment and is associated with subsequent poor survival during breeding on Samuel. That the flood of recruits on Samuel is not just a function of the high rate of reproduction is shown by the recruitment into the Saturna control population which had a lower reproductive rate but higher survival. If the Samuel population can produce almost double the number of litters, why is the density of deer mice on this island not comparable to that on Saturna?

The higher density on Saturna probably reflects a greater abundance of food in the virgin Douglas fir forest compared with that in the drier successional forest habitat on Samuel Island. This assumes that animals in both island populations are equally non-aggressive, but in no way implicates food as a factor limiting the number of mice on the smaller island. Young animals on Samuel have growth rates over two and one-half times those on Saturna, and this allows recruited animals to breed as soon as possible before the end of the breeding season. This is certainly reflected in the high number of recruits surviving to breed in the Samuel Island control population. Further evidence that food limitation is unlikely, is the success of introduced deer mice onto King Islet and Reef Island. Both these islands were dry and rocky with few trees and shrubs, but there obviously was enough edible material to support such high densities of mice. Redfield (pers. comm.) introduced cohorts of 50 mice to each of several previously uninhabited islands in the Gulf Islands, and all populations were thriving one year later.

The weather on the Gulf Islands is much less seasonal than on the mainland. Summers can be very dry, and so water could be a limiting factor on small rocky islands; but again the success of my introductions would appear to refute this hypothesis.

Predation appears as an unlikely source of mortality. No avian or terrestrial predators were observed on Samuel Island. Raccoons and herons were occasionally observed to forage in intertidal regions and mink are known to inhabit some of the smaller Gulf Islands, but were not seen on Samuel.

Thus, what is regulating the numbers of deer mice during the spring reorganization and breeding season on these islands? Aggressive behaviour by dominant animals cannot be ruled out. Comparison of demographic attributes in control and pulse populations showed no consistent differences throughout the study on the mainland and Saturna Island. Fairbairn (1976) found a similar result on the U.B.C. Endowment Lands, and concluded that the plasticity of these animals, in colonizing a vacant area and establishing a resident population, make deer mice very resilient to local extinctions. The situation on Samuel Island was somewhat different, as more males colonized the pulse removal grids; but the sex ratio stabilized at 1:1 in the succeeding pulse populations. Survival of males and females was significantly higher in nearly every pulse population compared with the control. This suggests that perhaps some animals, particularly males, may have been driven out of the resident population, and these possibly subordinate mice survived better on the depopulated areas. One might also expect growth rates to improve. However, males grew less and females slightly better than their control counterparts. There were no other consistent differences in demographic parameters between control and pulse populations on Samuel Island. There seems to be little difference in the plasticity of island and mainland mice colonizing vacant habitat.

I originally thought that if there were reduced dispersal on the islands, it would be a result of the 'island' or 'fence effect' (Krebs et al., 1969). With this lower rate of dispersal and movement, there might also be a reduction in aggressive

tendencies such that a population could survive successfully on a small, finite area of land. However, it seems unlikely that Saturna Island at 3102 ha (7680 acres) could act as an 'island' to a population of deer mice; and yet reduced dispersal on this island was comparable to that of Samuel with an area of 206 ha (510 acres). If dispersal is a function of island size, then it should be more restricted on islands smaller than Samuel, and more pronounced on larger areas such as Vancouver Island.

McCabe and Cowan (1945) reported lower densities of island Peromyscus spp. compared with nearby mainland areas further north in British Columbia. Redfield (1976) reported higher densities of deer mice on some of the Gulf Islands compared with the mainland of southwestern B.C. The 'fence effect' (Krebs et al., 1969) may be operating to reduce dispersal resulting in higher densities. This is in accordance with the condition of 'frustrated dispersal' suggested by Lidicker (1975). Populations of small mammals in experimental enclosures and on natural islands would cope with frustrated dispersal by increased usage of marginal habitat or a combination of decreased birth rate and increased death rate (Lidicker 1975).

Redfield (1976) has suggested that deer mice on the Gulf Islands are K-selected because of their larger body size and higher densities, which reflect different demographic parameters and reduced dispersal compared with mainland populations. Studies in Europe appear to support the contention that island populations of rodents tend towards K-selection. An island population of the Skomer vole (Clethrionomys glareolus skomerensis) exhibited larger body size, higher densities, very

short breeding season, and a slower maturation rate compared with populations on the British mainland (Fullagar et al., 1963; Jewell 1966). Populations of the long-tailed field mouse (Apodemus sylvaticus) on some British islands have larger body size than mainland animals but there is much variation among islands (Delany 1970). An island population of the bank vole (Clethrionomys glareolus) in Poland showed delayed maturation of young born late in the breeding season (Bujalska and Gliwicz 1968; Petruszewicz et al., 1971).

My island populations of Peromyscus maniculatus exhibit larger body size, higher densities, and reduced dispersal but they do not conform to the correlates of K-selection listed by Pianka (1970). In particular, mice on Samuel Island have rapid growth rates, a high reproductive rate, and poor survival which are all demographic correlates of r-selection. Deer mice on Saturna Island have higher growth rates, a slightly higher reproductive rate, and similar survival compared with mainland animals. Thus, compared with Samuel Island, mice on Saturna appear to be shifted towards the r-endpoint of the r-K continuum. Mainland populations of deer mice would probably also be located towards the K-endpoint compared with animals on Samuel Island.

Taxonomic studies of this species on the northern Gulf Islands (McCabe and Cowan 1945) and the Queen Charlotte Islands (Foster 1965) have indicated that there are several subspecies of deer mice on islands along the west coast of B.C. This information and the difference in body size and other external characteristics, such as pelage colour, between my island and

mainland populations, as well as the genetic variation shown by Redfield (1976), indicate that deer mice have probably been isolated on the islands for many thousands of years. Thus, evolutionary processes such as genetic drift could be responsible for the dispersal and recruitment pattern observed in these island mice. The effect of restricted land area may have interacted with the evolution of the populations. Regardless of the evolutionary origin of this dispersal and recruitment pattern, it may be concluded that on these islands seasonal changes in aggressiveness of the adult population may be sufficient but not necessary to determine the breeding density and seasonal changes in survival of juvenile deer mice. A more intensive study of seasonal changes in behaviour and the variation in demographic and dispersal parameters over several years for island populations of deer mice would rigorously test the validity of this conclusion. It perhaps can be stated with some credibility that regulatory processes in populations of Peromyscus maniculatus could be different in island populations and hence should not be generalized over different geographic areas.

SUMMARY

The demographic and dispersal results for island and mainland populations of deer mice in this study are summarized in Table 16.

Figure 1. Location of study areas: U.B.C. Research Forest at Maple Ridge, and Samuel Island, Saturna Island, Reef Island, and King Islet in the Gulf Islands.

Figure 2. Aerial photograph of island study areas: Samuel Island, Saturna Island, Reef Island, and King Islet.

Figure 3. Population density on mainland control and experimental grids, Peromyscus maniculatus. Non-breeding season is shaded. Vertical dotted bars represent start and end of breeding activity. Solid vertical bars enclose defined breeding season. Histograms indicate number of new males (shaded) and females (unshaded) recruited into control population.

MAINLAND CONTROL GRID P. MANICULATUS

MAINLAND PULSE REMOVAL GRID P. MANICULATUS

Figure 4. Population density on Samuel Island control and experimental grids, Peromyscus maniculatus. Non-breeding season is shaded. Vertical dotted bars represent start and end of breeding activity. Solid vertical bars enclose defined breeding season. Histograms indicate number of new males (shaded) and females (unshaded) recruited into control population.

SAMUEL ISLAND CONTROL GRID P. MANICULATUS

SAMUEL ISLAND PULSE REMOVAL GRID P. MANICULATUS

Figure 5. Population density on Saturna Island control and experimental grids, Peromyscus maniculatus. Non-breeding season is shaded. Vertical dotted bars represent start and end of breeding activity. Solid vertical bars enclose defined breeding season. Histograms indicate number of new males (shaded) and females (unshaded) recruited into control population.

SATURNA ISLAND CONTROL GRID *P. MANICULATUS* SATURNA ISLAND PULSE REMOVAL GRID *P. MANICULATUS*

Figure 6. Minimum survival rates per 14 days for Peromyscus maniculatus on the mainland, Samuel Island, and Saturna Island control grids. Non-breeding season is shaded. Vertical dotted bars represent start and end of breeding activity. Solid vertical bars enclose defined breeding season. Males and females are shown separately.

MAINLAND CONTROL GRID P. MANICOLLATUS

Figure 6(continued):

53a

SAMUEL ISLAND CONTROL GRID P. MANICULATUS

SATURNIA ISLAND CONTROL GRID P. MANICULATUS

Figure 7. Overlapping histograms of percentage of animals sexually mature in various body weight classes for the three study areas. Males and females are combined.

Mainland

Samuel Island

Saturna Island

Figure 8. Body weight distributions for breeding (summer - June to Aug.) and non-breeding (winter - Dec. To Feb.) seasons for male Peromyscus maniculatus in the three control populations.

MAINLAND CONTROL GRID SUMMER

MAINLAND CONTROL GRID WINTER

SAMUEL ISLAND CONTROL GRID SUMMER

SAMUEL ISLAND CONTROL GRID WINTER

SATURNA ISLAND CONTROL GRID SUMMER

SATURNA ISLAND CONTROL GRID WINTER

WEIGHT CLASS g

WEIGHT CLASS g

Figure 9. Mean growth rates with 95% confidence limits for control and experimental populations of Peromyscus maniculatus for the four pulse periods. Control represented by closed circle and experimental by open circle. Sample size above upper confidence limits.

GROWTH RATES CONTROL AND EXPERIMENTAL GRIDS MALES *P. MANICOLLATUS* GROWTH RATES CONTROL AND EXPERIMENTAL GRIDS FEMALES *P. MANICOLLATUS*

Figure 10. Median body weight at sexual maturity and 95% confidence limits for males and females from each study area during the period June to Aug. 1974. Control populations represented by closed circle and experimentals by open circle.

MEDIAN BODY WEIGHT AT SEXUAL MATURITY FOR MALES AND FEMALES *P. MANICULATUS*

Grid Designations:

- A - mainland control
- B - mainland pulse removal
- C - Samuel Island control
- D - Samuel Island pulse removal
- E - Saturna Island control
- F - Saturna Island pulse removal

Figure 11. Schematic representation of seasonal changes in populations of Peromyscus maniculatus. Model based on research of Sadleir (1965), Healey (1967), and Fairbairn (1976).

Table 1. Trappability estimates for Peromyscus maniculatus on the three control areas for this study. Sample size in parentheses. Maximum trappability is the proportion of those known to be alive that are actually caught in a trapping session. Minimum unweighted trappability eliminates first and last captures and provides only one value for each individual regardless of how long he lives.

	Mainland		Samuel Island		Saturna Island	
	Males	Females	Males	Females	Males	Females
Maximum Trappability	0.91 (44)	0.79 (34)	0.96 (95)	0.94 (73)	0.80 (103)	0.84 (75)
Minimum Unweighted Trappability	0.87 (29)	0.72 (23)	0.86 (34)	0.85 (39)	0.69 (66)	0.77 (46)

Table 2. Comparison of adult and juvenile recruitment during removal weeks in the breeding season. Males and females are shown for control and pulse removal grids of each study area.

	Adults				Juveniles		
	Males	Females	Total		Males	Females	Total
Mainland							
Removal No. 2 (Aug. 14-16; Aug. 28-30)	5	2	7		14	8	22
Control	0	0	0		3	0	3
Samuel Island							
Removal No. 2 (Aug. 12-14; Aug. 26-28)	10	1	11		9	10	19
Control	1	1	2		10	5	15
Removal No. 3 (Nov. 1-2; Nov. 15-16)	5	1	6		14	10	24
Control	1	1	2		13	4	17
Saturna Island							
Removal No. 2 (Aug. 12-14; Aug. 26-28)	6	2	8		19	22	41
Control	3	2	5		10	9	19

Table 3. Population density for control populations and colonization data for the removal weeks in each removal period, Peromyscus maniculatus. 66

		Control population	Experimental population			
		Density	No. immigrants	Recovery ratio (control)	Recovery ratio (pre-removal)	Relative recruitment index
Mainland	week					
Removal No. 1.	1st	7	10	142.8	100.0	7.33
	2nd	9	12	133.3	120.0	
Removal No. 2.	1st	17	17	100.0	130.8	9.67
	2nd	16	12	75.0	92.3	
Removal No. 3.	1st	25	16	64.0	72.7	7.75
	2nd	25	15	60.0	68.2	
Removal No. 4.	1st	21	0	0.0	0.0	-
	2nd	17	4	23.5	44.4	
Mean value(Removal Nos. 1,2,+3)				95.8	97.4	8.25
95% confidence limits				58.4-133.2	71.1-123.6	
Samuel Island	week					
Removal No. 1.	1st	10	8	80.0	50.0	3.67
	2nd	8	3	37.5	18.8	
Removal No. 2.	1st	22	16	72.7	69.6	1.76
	2nd	19	14	73.7	60.9	
Removal No. 3.	1st	21	17	81.0	70.8	1.58
	2nd	35	13	37.1	54.2	
Removal No. 4.	1st	30	13	43.3	72.2	3.71
	2nd	29	13	44.8	72.2	
Removal No. 5.	1st	27	13	48.2	65.0	6.50
	2nd	24	13	54.2	65.0	
Mean value				57.3	59.9	3.44
95% confidence limits				44.6-70.0	48.2-71.5	
Saturna Island	week					
Removal No. 1.	1st	36	20	55.6	58.8	1.63
	2nd	41	6	14.6	17.6	
Removal No. 2.	1st	39	27	69.2	103.8	2.04
	2nd	51	22	43.1	84.6	
Removal No. 3.	1st	48	13	27.1	28.9	6.75
	2nd	49	14	28.6	31.1	
Removal No. 4.	1st	44	4	9.1	15.4	16.00
	2nd	45	12	26.7	46.2	
Removal No. 5.	1st	47	19	40.4	61.3	2.78
	2nd	38	6	15.8	19.4	
Mean value(Removal Nos. 1,2,3,+5)				36.8	50.7	3.30
95% confidence limits				21.0-52.7	24.1-77.3	

Table 4. Results of Analysis of Covariance of observed range length regressed on number of times captured for males and females. Means compared by Duncan's Multiple Range Tests(D. M. R. T.).

Males

Source	F value	Probability
Area	5.39	0.0001

D. M. R. T.(p=.05) Any means underscored by the same line are not significantly different from one another.

	E	F	A	C	D	B
Average Observed Range Length (m)	34.0	37.8	40.9	45.0	49.1	54.9
N=number of animals	81	84	35	59	57	34

Females

Source	F value	Probability
Area	5.36	0.0001

D. M. R. T. (p=.05) Any means underscored by the same line are not significantly different from one another.

	F	C	E	D	B	A
Average Observed Range Length (m)	32.5	35.6	36.4	36.8	45.6	51.3
N=number of animals	72	55	60	44	28	27

Grid Designations:

- A - mainland control
- B - mainland pulse removal
- C - Samuel control
- D - Samuel pulse removal
- E - Saturna control
- F - Saturna pulse removal

Table 5. Proportion of Peromyscus maniculatus in breeding condition on control areas during a comparable period of the breeding season. Sample size in parentheses.

Season and Group	Mainland	Samuel Island	Saturna Island	Comparisons		
	(A)	(C)	(E)	A-C	A-E	C-E
June - August 1974						
Testes Scrotal						
Adults	.80 (46)	.91 (23)	.67 (75)			C-E**
Juveniles	.14 (7) ⁺	.12 (26)	.02 (43)			
Vagina Perforate						
Adults	.15 (48)	.22 (32)	.15 (78)			
Juveniles	.25 (4) ⁺	.17 (18)	.13 (23)			
Nipples Med.-Large						
Adults	.71 (48)	.81 (32)	.62 (78)			C-E*

* $p < .05$ significant difference by Chi-square

** $p < .01$

+ inadequate sample size to test for difference

Table 6. Proportion of Peromyscus maniculatus in breeding condition on control and experimental areas for week of colonization following each removal during the breeding season. Totals for adults and juveniles are shown for each area. Sample size in parentheses.

Group	Mainland		Samuel Island		Saturna Island	
	Control	Removal	Control	Removal	Control	Removal
Testes Scrotal						
Adults	1.00 (10)	1.00 (5)	0.83 (24)	0.79 (29)	0.70 (89)	0.74 (31)
Juveniles	0.00 (5)	0.21 (14)	0.00 (30)	0.05 (21)	0.09 (44)	0.11 (28)
Vagina Perforate						
Adults	0.00 (15)	0.00 (5)	0.16 (38)	0.36 (14)	0.20 (54)	0.38 (8)
Juveniles	0.00 (0)	0.00 (8)	0.14 (14)	0.06 (16)	0.10 (39)	0.16 (43)
Nipples Med.-Large						
Adults	0.80 (15)	1.00 (5)	0.68 (38)	0.71 (14)	0.28 (54)	0.13 (8)

Table 7. Comparison of proportion of animals in breeding condition for control and experimental populations during the first and second Pulse Periods. Sample size in parentheses.

Period and Group	Mainland		Samuel Island		Saturna Island	
	Control	Removal	Control	Removal	Control	Removal
Pulse No. 1.						
Testes scrotal						
Adults	0.75 (36)	0.77 (30)	0.94 (17)	0.93 (30)	0.73 (52)*	0.92 (36)
Juveniles	0.50 (2) ⁺	0.20 (5) ⁺	0.25 (12) ⁺	0.00 (6) ⁺	0.05 (20)	0.13 (8) ⁺
Vagina perforate						
Adults	0.21 (33)	0.18 (22)	0.20 (20)	0.15 (20)	0.18 (56)	0.17 (22)
Juveniles	0.25 (4) ⁺	0.67 (3) ⁺	0.27 (11)	0.50 (6) ⁺	0.27 (11)	0.23 (13)
Nipples med.-large						
Adults	0.67 (33)	0.41 (22)	0.90 (20)	0.75 (20)	0.68 (56)	0.86 (22)
Pulse No. 2.						
Testes scrotal						
Adults	0.26 (19)	0.20 (15)	0.65 (20)*	0.91 (33)	0.30 (56)**	0.64 (22)
Juveniles	0.00 (49)	0.03 (34)	0.13 (30)	0.25 (8) ⁺	0.02 (60)	0.02 (53)
Vagina perforate						
Adults	0.03 (29)	0.00 (15)	0.23 (35)	0.20 (35)	0.11 (38)	0.18 (11)
Juveniles	0.00 (15)	0.00 (27)	0.00 (23)	0.22 (9) ⁺	0.00 (54)	0.02 (50)
Nipples med.-large						
Adults	0.45 (29)	0.53 (15)	0.71 (35)	0.57 (35)	0.42 (38)*	0.09 (11)
Total						
Testes scrotal						
Adults	0.58 (55)	0.58 (45)	0.78 (37)*	0.92 (63)	0.51 (108)**	0.81 (58)
Juveniles	0.02 (51)	0.05 (39)	0.17 (42)	0.14 (14)	0.03 (80)	0.03 (61)
Vagina perforate						
Adults	0.13 (62)	0.11 (37)	0.22 (55)	0.18 (55)	0.15 (94)	0.15 (33)
Juveniles	0.05 (19)	0.07 (30)	0.09 (34)	0.33 (15) ⁺	0.05 (65)	0.06 (63)
Nipples med.-large						
Adults	0.56 (62)	0.46 (37)	0.78 (55)	0.64 (55)	0.57 (94)	0.61 (33)

* $p < .05$ ** $p < .01$ significant difference by Chi-square between control and removal samples

+ inadequate sample size to test for difference

Table 8. Minimum survival rates per 14 days for the three control populations.
Sample size in parentheses.

Season and Group	Mainland (A)	Samuel Island (C)	Saturna Island (E)	Comparisons		
				A-C	A-E	C-E
Males						
Winter 1974						
Total	0.89 (18) ⁺	0.86 (7) ⁺	0.84 (68) ⁺			
Summer 1974						
Total	0.76 (45)	0.64 (160)	0.79 (153)			C-E**
Adults	0.76 (41)	0.69 (88)	0.84 (100)			C-E*
Juveniles	0.75 (4) ⁺	0.58 (72)	0.70 (53)			
Winter 1974-75						
Total	0.87 (146)	0.80 (120)	0.90 (210)			C-E**
Summer 1975						
Total	-	-	0.89 (120)			
Total	0.85 (209)	0.71 (287)	0.86 (551)	A-C**		C-E**
Females						
Winter 1974						
Total	0.56 (9) ⁺	1.00 (7) ⁺	0.81 (48)			
Summer 1974						
Total	0.87 (45)	0.73 (160)	0.87 (125)			C-E**
Adults	0.88 (41)	0.82 (104)	0.85 (87)			
Juveniles	0.75 (4) ⁺	0.57 (56)	0.92 (38)			C-E**
Winter 1974-75						
Total	0.87 (97)	0.87 (122)	0.88 (150)			
Summer 1975						
Total	-	-	0.84 (69)			
Total	0.85 (151)	0.80 (289)	0.86 (392)			C-E*

* $p < .05$ significant difference by Chi-square

** $p < .01$

+ inadequate sample size to test for difference

Table 9. Indices of early juvenile survival and reproductive data for the three control populations. Ranges for indices of survival based on samples including 2 or more females. Sample size in parentheses for observed proportion of juveniles surviving and surviving to breed. N= number of trapping weeks.

	Mainland			Samuel Island			Saturna Island		
	Mean	N	Range	Mean	N	Range	Mean	N	Range
Breeding season 1974	0.14	6	0-0.29	1.46	18	0-2.75	0.98	9	0.25-4.5
Breeding Season + to end of recruitment	0.66	11	0-2.00	1.49	20	0-2.75	1.00	14	0-4.5
Litter size	4.52*	57	3.36-5.68	3.38 ⁺	32	2-5	3.38 ⁺	32	2-5
Number of successful pregnancies	Total	N	Range	Total	N	Range	Total	N	Range
	13	7	1-4	33	15	1-12	18	13	1-3
Expected number of juveniles	58.8			111.5			60.8		
Observed number of juveniles	3			92			44		
Proportion surviving ¹	Males		Females	Males		Females	Males		Females
	0.67 (3)		0	0.46 (35)		0.50 (30)	0.60 (20)		0.75 (8)
Proportion surviving and breeding ²	0.00		0	0.29 (35)		0.47 (30)	0.00 (20)		0.38 (8)

* Sadleir 1974

+ laboratory litters from Saturna Island

¹ animals caught up to one month before end of breeding and survive at least two weeks

² animals in reproductive condition before end of breeding

Table 10. Comparison of minimum survival rates per 14 days for control and experimental populations during Pulse Periods. Sample size in parentheses.

Period and Group	Mainland		Samuel Island		Saturna Island	
	Control	Removal	Control	Removal	Control	Removal
Males						
Pulse No. 1.						
Total	0.74 (31)	0.85 (27)	0.50 (24) **	0.88 (26)	0.67 (58)	0.73 (33)
Pulse No. 2.						
Total	0.96 (48)	0.93 (40)	0.62 (42)	0.72 (32)	0.90 (98)	0.93 (58)
Pulse No. 3.						
Total	0.83 (30) *	0.54 (13) +	0.64 (55) *	0.90 (29)	0.95 (66)	0.94 (31)
Pulse No. 4.						
Total	0.89 (19)	1.00 (13)	0.84 (49)	0.85 (41)	0.89 (66)	0.96 (25)
Total	0.87 (128)	0.86 (93)	0.67 (170) **	0.84 (128)	0.86 (288)	0.89 (147)
Females						
Pulse No. 1.						
Total	0.92 (26)	0.86 (22)	0.59 (22) *	0.95 (17)	0.79 (56)	0.69 (26)
Pulse No. 2.						
Total	0.88 (33)	0.84 (32)	0.70 (46) **	1.00 (29)	0.89 (73)	0.93 (41)
Pulse No. 3.						
Total	0.96 (23) **	0.54 (13) +	0.64 (39) **	1.00 (14)	0.91 (44)	0.96 (25)
Pulse No. 4.						
Total	0.80 (15)	1.00 (2) +	0.95 (58)	0.86 (28)	0.92 (38)	0.95 (21)
Total	0.90 (97)	0.80 (69)	0.76 (165) **	0.94 (88)	0.87 (211)	0.88 (113)

* $p < .05$

** $p < .01$ significant difference by Chi-square between control and removal samples

+ inadequate sample size to test for difference

Table 11. Age classes of animals, based on body weight.

Study Area	Weight(grams)		
	Juveniles	Subadults	Adults
Mainland	0 - 12g	13 - 16g	≥17g
Samuel Island	0 - 12g	13 - 18g	≥19g
Saturna Island	0 - 14g	15 - 20g	≥21g

Table 12. Analysis of Covariance for growth rates regressed on body weight of animals < 20 g for the period June to Oct. 1974. Males and females are combined. Mean growth rates are given with sample size in parentheses. F values and probabilities for comparisons of three study areas are also shown.

	Mainland (A)	Samuel Island (C)	Saturna Island (E)
Growth Rate	0.0020 (124)	0.0111 (47)	0.0040 (108)
Comparisons	F value		Probability
A - C	59.9		0.00
A - E	4.9		0.03
C - E	25.3		0.00

Table 13. Sex ratios (proportion of males) in control and experimental populations of Peromyscus maniculatus. Sample size in parentheses.

Period	Mainland		Samuel Island		Saturna Island	
	Control	Removal	Control	Removal	Control	Removal
Removal No. 1.	0.69 (16)	0.59 (22)	0.41 (17)	0.73 (11)	0.57 (65)	0.42 (26)
Removal No. 2.	0.50 (30)	0.61 (31)	0.51 (39)	0.63 (30)	0.58 (80)	0.51 (49)
Removal No. 3.	0.67 (46)	0.61 (31)	0.54 (50)	0.63 (30)	0.52 (61)	0.52 (27)
Removal No. 4.	0.65 (26)	1.00 (4)	0.50 (52)	0.62 (26)	0.63 (49)	0.69 (16)
Removal No. 5.	-	-	0.53 (45)	0.58 (26)	0.62 (81)	0.63 (25)
Total	0.63 (118)	0.63 (88)	0.51 (203)	* 0.63 (123)	0.58 (336)	0.55 (143)

* $p < .05$ significant difference by Chi-square between control and removal samples

Table 14. Results of introductions of island and mainland mice onto King Islet(0.4 acre) and Reef Island(4.0 acres).

King Islet	May 10			July 29-31 (100 trap nights)		
	Males	Females	Total	Males	Females	Total
Mainland Mice	2	2	4	2	1	3
Island Mice	2	2	4	2	1	3
				(17 untagged offspring)		
King Islet	July 31			Oct. 18-20 (155 trap nights)		
	Males	Females	Total	Males	Females	Total
Mainland Mice	26	7	33	12	1	13
Island Mice	20	14	34	12	8	20
				(15 untagged offspring)		
Reef Island	May 10			July 29-31 (200 trap nights)		
	Males	Females	Total	Males	Females	Total
Mainland Mice	22	18	40	20	12	32
Island Mice	21	18	39	14	13	27
				(27 untagged offspring)		

Table 15. Results of behaviour tests for breeding males, Peromyscus maniculatus, from Samuel Island and Saturna Island. Mean number and range of 5 second intervals (maximum of 120) of each behaviour for N=7 encounters are given for each island.

Behaviour	Samuel Island		Saturna Island	
	Mean	Range	Mean	Range
Latency period/10 min.	2.8	1-6	8.7	4-10
<u>Aggressive Behaviour</u>				
Upright	2.7	0-13	1.7	0-5
Box	0.0	-	0.3	0-2
Avoid	0.7	0-5	0.0	-
Avoid leap	0.14	0-1	0.0	-
Threat	0.0	-	0.0	-
Fight	0.0	-	0.14	0-1
<u>Cohesive Behaviour</u>				
Approach	12.1	0-22	7.0	1-12
Nose to nose + mutual sniff	6.1	0-16	3.4	0-8
Sniff	16.1	0-38	6.4	1-15
Huddle-contact	9.3	0-32	5.1	0-30
Total (Number of 5 second intervals in which animals interacted)	35.9	0-63	17.4	1-53

Table 16. Summary of demography and dispersal in island and mainland populations of deer mice.

	Mainland	Samuel Island	Saturna Island
Average density (per hectare)	18.7	22.0	43.5
Reproductive rate (1974)			
- length of breeding season (weeks)	12	34	18
- number of successful pregnancies	13	33	18
- proportion of (males)	0.80	0.91	0.67
breeding animals < (females)	0.71	0.81	0.62
- proportion of recruits surviving to breed	0	0.37	0.11
Survival (adults and juveniles)			
males (summer)	0.76	0.64	0.79
(winter)	0.87	0.80	0.90
females (summer)	0.87	0.73	0.87
(winter)	0.87	0.87	0.88
Relative growth rates	1.0	5.6	2.0
Body size (adults)	≥17 g	≥19 g	≥21 g
Dispersal (colonization rate)			
- mean recovery ratio(to control population)	95.8	57.3	36.8
- mean recovery ratio(to pulse population)	97.4	59.9	50.7
- mean relative recruitment index	7.3	3.6	3.5
- observed range length (m)			
(males)	40.9	45.0	34.0
(females)	51.3	35.6	36.4
No. recruits per trapping week of breeding season			
(males)	1.0	2.9	3.1
(females)	0	2.2	1.8
Behaviour (breeding season)	more aggressive (Sadleir 1965) (Healey 1967) (Fairbairn 1976)	less aggressive	less aggressive

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