"There is no more common error than to assume that,
because prolonged and accurate mathematical calculations
have been made, the application of the result to some
fact of nature is absolutely certain."

Alfred North Whitehead.

POPULATION DYNAMICS AND BEHAVIOUR OF DEERMICE IN

A COASTAL FOREST OF BRITISH COLUMBIA

By

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ABSTRACT

A two year live trapping study of deermice, <u>Peromyscus</u> <u>maniculatus</u>, was carried out on the University of British Columbia Research Forest at Maple Ridge, B.C., starting in the fall of 1968. Monthly trapping was conducted on three one hectare grids representing different vegetational succession stages in relation to logging; area 1 - a 100 year stand of Douglas fir; area 2 - an area logged in summer 1968; area 3 - an area logged in 1964 and planted in 1965. All areas were at an altitude of between 150 and 200 metres and within 1.7 kilometres of each other. The study was designed to monitor the relative importance of habitat differences and extrinsic and intrinsic factors which could affect populations over large areas.

Capture-recapture data was analysed by using Jolly's stochastic model, which gave estimates of total numbers (N), probability of survival (ϕ), and recruitment (B). Populations on all three areas followed similar trends in these parameters but the numbers on areas 1 and 2 were generally higher than on area 3. The population of deermice on area 3 vanished in August 1970. There were considerable differences between the years in the pattern of population fluctuations. Numbers were highest in 1969. Comparisons of the total number, probability of survival, and recruitment estimates indicated that the main factor determining population change was the length of the non-breeding season, in particular as it affected recruitment.

Home ranges of particular animals were compared by the live
trapping minimum area method and by the smoked paper toe-clipping
technique. It was not possible to compare home range between areas
because the apparent home range increased with capture frequency.
Males in breeding condition occupied larger home ranges than non-breeding males
or females at any time of the year. The smoked paper toe-clipping
technique gave a much better estimate of home range and movements than
trapping.

Agonistic behaviour of males was studied on area 2, from January
1970, by determining the number of aggressive acts between field
individuals in paired bouts. Aggression increased to a peak in June
and then declined. This was confirmed by the movement patterns revealed
by the smoked paper studies. Although only a small number of males were
monitored on a sufficient number of occasions, there appeared to be a
strong relationship between the level of aggressive behaviour and size
of home range.

Control of this species in relation to reseeding is discussed.

ACKNOWLEDGEMENTS

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CHAPTER 1

GENERAL INTRODUCTION

The deermouse, Peromyscus, has a wide distribution over the North

American continent. Osgood (1909) stated "... it is probable that a line

or several lines could be drawn from Labrador to Alaska and hence to

Southern Mexico through which not a single mile is not inhabited by some

form of this species." And this is almost certainly still correct. Deermice

usually inhabit woodland and bushland areas but may occur in open areas of mixed

weeds and grasses characteristic of pioneer stages of grassland development.

However, in these latter areas, Peromyscus are usually secondary to Microtus

or other microtines, especially in the north temperate and boreal regions.

In the west coast rain forest (Krajina, 1970) of the mainland and

coastal islands of British Columbia, there are twenty-four subspecies of

Peromyscus (Cowan and Guiget, 1965). In the general area where this study

was conducted the species concerned was Peromyscus maniculatus austerus.

There is another species, P. oreas, which also occurs in this region and

cases of interbreeding between these two species have been reported

(Osgood, 1909). Sheppe (1961) has shown that P. oreas and P. maniculatus

are reproductively and spatially isolated in the study area. This study

was conducted entirely in the area which Sheppe designated as the range

of P. m. austerus (Fig. 1).

Practically all knowledge of small mammal population parameters such

as movement, home range, activity rhythms, and spatial distribution

have been determined by live traps. The estimation of these parameters as

Fig. 1   Map of University of British Columbia Research

                  Forest, Maple Ridge, indicating location of grids.

U.B.C. RESEARCH FOREST

LOON
LAKE

MARION
LAKE

F

E

E

BLANEY
LAKE

BLANEY CREEK

ALOUETTE RIVER

K

G

G40

G10

Q

GRID
2

GRID
1

GRID
3

F

A

A 20

N

232 St.

4000 feet

485 meters

– – – – ROAD

– ·· – ·· FOREST BOUNDARY
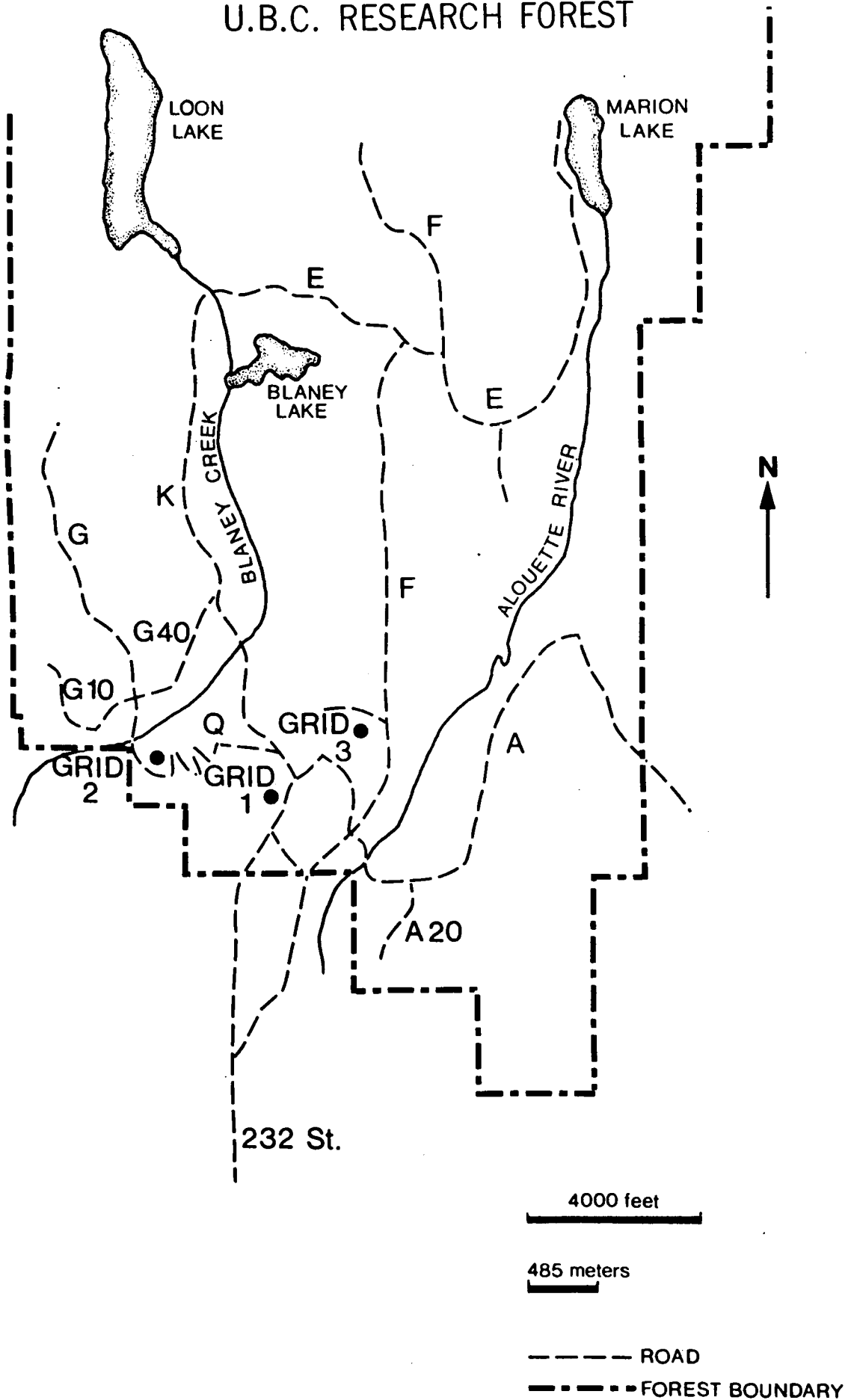
well as the dynamic aspects of the population is entirely "dependent

upon trapping and involves some basic assumptions for which evidence

is not universally established" (Kikkawa, 1964). For example, the basic

assumption common to many formulae used to estimate population size

from trapping data is that all individuals have the same probability of

being captured in any sample period. In fact, trapping

procedures affect this probability and some of this bias can be detected

in trapping results (Kikkawa, 1964; Tanton, 1965). They arise because

certain biological characteristics of the population prevent random

sampling and are dependent on and vary with trapping procedure. Such bias

may be attributed to (summarized in part from Kikkawa (1964)):

(a) trapping interval - this may affect parameters such as weight

distribution, the proportion of animals of which grow to trappable size

and die or immigrate before being sampled, the proportion of animals which

pass through the area unnoticed or those which move on or off the grid

between trapping periods. The latter two biases can be generally classified

as dispersal as defined by Leslie, Chitty, and Chitty (1953).

(b) trap spacing - this affects the sampling of individuals because as

traps are spaced farther apart the probability of an individual encountering

a trap within its home range diminishes. However, Hayne (1950) found for

Microtus, that increasing the distance between traps tended to increase

the apparent area and consequently distorted its original home range.

(c) reaction to traps - the population includes individuals whose behaviour

ranges from those which never enter traps because they are trap shy, to those so

addicted that they enter traps at every possible occasion. This differential response may diminish with repeated exposure to traps or may be enhanced after the initial encounter. There may also be social factors which favour certain individuals such as in sexual differences, that is, sex ratios (Davis, 1955; Tanton, 1965), age groups (Davis and Emlen, 1956), or interspecific differences. Superimposed on all these above factors are the type of bait used, the activity rhythm of the species concerned and the presence and numbers of other trappable species - all of which vary according to day length, food supply, and weather (Calhoun, 1945). Therefore, any attempt to establish the relationship between samples and population will have to consider trap response in relation to trapping procedure.

This study was conducted, in the University of British Columbia Research Forest at Maple Ridge, B.C., on three one hectare grids which were located in different forest habitats. Vegetation on these areas was described by Petticrew and Sadleir (1970) and Kellman (1969). The grids were chosen in relation to their vegetational stage of development after logging, since one of the concerns of this study was the effect of present and past logging operations and burning on small mammal populations.

This project was designed to study the home range and population dynamics of P. m. austerus in three specific areas. It was hoped that the use of multiple grids (instead of a single grid) would allow the construction of a general population model which could explain population changes over a general area and that this model would be consistent with

all three populations. The study also compared the stability of
home range in relation to varying environments. An additional
study of the behaviour of feral deermice on one particular grid was
undertaken and analysed as to its conformity to the agonistic population
control theories of Sadleir (1965). It was also hoped that a general
overview of the total study could be made of the effects of the drastic
environmental changes caused by logging on the mouse populations, as
well as suggesting means of control for this seed eating species. It was
envisaged that the findings of this study could then become the basis for
recommendations as to the means and timing of the control of deermice as
a forest pest.

CHAPTER 2

INTRODUCTION - HOME RANGE

Individuals of most mammal species do not wander at random but confine their activities to limited areas or home ranges. This enables each individual or social group to become familiar with its own area - the physical structure, resources, predators as well as the presence of the other members or groups of the same species. Seton (1910) has often been quoted for his descriptions of the home range or home area of mammals whilst Darling (1937) wrote of these areas as territories. However, Burt (1940, 1943) advocated separate uses for these terms. He considered the home range to be that area around the established home which is traversed by the animal in its normal activities of food gathering, mating, and caring for the young. This excludes occasional sallies outside the area. Burt considered territory as any defended area. Later Burt (1946) described three categories of home range: permanent, semi-permanent, and seasonal. Small mammals have home ranges of the first two types. Hayne's (1949) concept of home range differed from that of Burt as he conceived of home range in a mathematical sense as being limited not by fixed lines but by statistical zones of decreasing probability of occurrence. Jewell (1966) defined home range as an area with a certain productivity that meets the energy requirements of the individual or group that occupies it. The difficulty in defining home range precisely in a physical sense stems largely from the fact that one is attempting to state in static terms (that is, in square feet or fractions of acres), the area of activity of a living mobile animal that may have its movements

influenced by a great many factors in the physical and biological environment.

Except at special times in its life history, for example, the dispersal that occurs at the onset of sexual maturity, small mammals remain within their established home ranges. There is a proportion of the small mammal population, the transients, which does not become established. In fact, Andrzejewski (1962) has suggested that small mammal populations consist of two parts, residents and transients (Andrzejewski and Wierzbowska, 1961; Andrzejewski and Wroclawek, 1962). The proportion of animals that are in transit varies, and it is rarely possible to determine whether captured transients are on exploratory trips from home areas outside the trapping area or whether they are individuals who have never succeeded in establishing ranges anywhere. Stickel and Warbach (1960) found that 79 percent of a population of <u>Peromyscus leucopus noveboracensis</u> had relatively stable home ranges, remaining in the same general area from month to month, while the remaining 21 percent were considered to be transient. Youngmen (1956) noted that there was a seasonal variation in the number of transients. He found that the proportion of transients in an <u>Apodemus agarius</u> population was higher in February (35.84%) than in May (21.51%). When the resident population was reduced, transients took the place of residents and their proportion fell to 14.28 percent.

Home range is more than just the area that a rodent happens to occupy. Each individual has a positive relationship to its range as shown by the frequency with which they return when removed from their ranges and released away from it (Sheppe, 1966). The home range concept allows one

to evaluate the relative importance of the factors that influence a
population. These include the number of individuals, the biomass of the
community, the growth of the individual, the social stability of the group,
and the "psychological well-being" of the individual (Calhoun, 1952). The
effects of physical parameters such as habitat and food supply on home
range size are difficult to evaluate. Stickel (1948) has attempted to
show that the size of the home range area may be influenced by the diversity
of the habitat, although in field studies it usually has not been possible
to separate habitat differences from the effects of other factors such as
food and population density. She determined that Peromyscus gossypinus
had home ranges of very similar size in burned and unburned plots of pine
(Pinus) in Louisiana, and that P. leucopus noveboracensis living in
unproductive pine-oak association had larger home ranges than mice living
in the bottomlands where food was more plentiful. No definite relationship
between home range size and food supply has been established in mammals,
although such relationships have been proposed for birds (Watson, 1964).
However, it has been shown that mice living in corn stocks where food was
abundant travelled much shorter distances than mice living in open fields
of wheat stubble (Linduska, 1942).

The individuals constituting a population of small mammals are
part of an organized society. The position of an individual in the
structure of such a society will affect its behaviour and thus its move-
ments over the home area. In each group of Apodemus sylvaticus living
within a specific area, there is a single dominant male who ranges more
widely than any of its subordinates (Brown, 1966). Although such a
system has not yet been found in Peromyscus maniculatus populations

in a natural habitat, Sadleir (1970a) has demonstrated that a dominance hierarchy can last for more than a month in a laboratory colony of P. maniculatus.

Sanderson (1966) has excellently reviewed most of the techniques used to study mammal movements. He uses the term "movements" in a broad sense including activity, home range, immigration, emigration, and movements associated with behavioural changes. Movement data can be collected by direct and indirect methods. Direct observations of mammals are advantageous in that they minimize handling, do not hamper individual movement, and enable immediate information on where an animal is and what it is doing to be gathered. The disadvantages of the technique are the time required, the limited number of individuals that can be observed at one time, and the influence, if any, of the observer on the behaviour of the individual being studied. Indirect methods include the use of natural signs such as tracks, feces (Murie, 1936; Scott, 1943); capture, mark, release, and recapture methods (Chitty, 1937; Burt, 1940; Howard, 1949; Blair, 1951); radioactive marking techniques (Godfrey, 1954; Kaye, 1960, 1961); the use of dyes to mark urine and feces (New, 1958; Kindel, 1960; Brown, 1961; Brown and Conaway, 1961); smoked paper (Justice, 1961); photographic devices (Pearson, 1960; Voisey and Kalbfleisch, 1962); radiotelemetry (Storm, 1965; Cochran, Warner, Tester, and Kuechle, 1965). As Sanderson (1966) has pointed out, however, the techniques involved in locating and observing mammals appear to be far ahead of the systems available for

interpreting the data. No one technique for determining location and no system for analyzing data can give an accurate picture for all species and all situations. The influence of the length of the observation period has rarely been considered in calculating home ranges or distances of movement (Sanderson, 1966). Techniques for analyzing home range data are many: the minimum area method, the boundary strip method, the inclusive boundary strip method, the observed range length, and the adjusted range length. Van Vleck (1969) has described in detail the advantages and disadvantages of using the above methods. Other methods are the centre of activity, activity radii, recapture radius, standard diameter, and standard range. The biological significance of each method is difficult to determine.

Most information about the home ranges of small nocturnal mammals has come from records of repeated captures of marked individuals in live traps. Repeated captures of an individual establishes points that limit the area of the estimated range of that animal. This estimate of home range size is certainly a crude estimate of the actual area ranged over and only in the rarest of circumstances will the estimated home range correspond exactly to the area of movement of the animal. In most studies the estimation of home range has been a by-product of trapping to estimate the numbers of a specific population. Consequently all early estimates of home range size were trap determined. Dalke and Sime (1938) suggested the minimum area method for the determination of home range size. They assumed that every point at which an animal was captured was the furthest extent of his range in that particular direction. Each point of capture

was connected by straight lines and the enclosed area measured. Modifications of this method resulted in the boundary strip and the inclusive boundary strip methods of estimation. Each of these methods is similar to the minimum area method except that in the latter method a correction factor is added (Stickel, 1954). However, the corrections are merely arbitrary and although they may give larger estimates of home range size they bear no biological significance to the true range of the animal.

METHODS

Determination of Home Range

(a) Field Techniques

The location of animals inside their home range was determined by trapping and by the smoked paper-toe clipping technique described by Justice (1961) and Sheppe (1965). Trap revealed home range was determined on all grids from September 1968 through to September 1970 (whereas the latter technique was employed only on Area 2 from January through to September 1970). The grids are described in more detail on pages 3 and 32.

Strips of waterproof paper were smoked using a benzene flame. Each strip of smoked paper was then placed in a quart size milk carton from which the ends had been removed, forming a tunnel. Cartons were placed within 2 m of every 10 m stake on the grid. When these milk carton tunnels had been in place overnight footprints of particular toe-clipped males were discernible on many of the smoked paper surfaces (Plate 1). These cartons were set out on day 4 and picked up on day 5 of every trapping week.

Plate 1   Photograph of tracks of deermice through a

smoked paper carton. This animal was toe clipped

number 11.

Toe clipping involved the removal of certain digits on the fore and hind feet of deermice. The digits on the front feet represented the units ranging from one to eight, those on the hind feet represented the tens ranging from ten to one hundred, i.e. total of eight toes on the front feet and ten on the hind feet. Therefore if the second digit on the right front foot and the second digit on the right rear foot had been removed then the toe clipped number for this specific mouse was 2 plus 20 equals 22 (see Plate 1). Thus, ninety-eight mice could be marked individually using this system.

(b) Analysis of data

Home range determinations for the trap determined, smoked paper, and the combined methods were calculated using the minimum area method (Dalke and Sime, 1938). This method assumes that the most extreme points of capture of an individual animal defines the outermost limits of its home range. Ranges were determined for animals which were captured on more than three separate occasions at capture sites which were nonlinear in distribution. Edge trapped animals were excluded if they were captured more than 25% of the time on the peripheral rows and columns of the grid. All home range areas were averaged and grouped according to the sex and breeding status of the mice.

RESULTS

1) <u>Determination of the number of captures needed to determine home range size</u>

Fig. 2 shows the home range areas as a function of the number of captures for males and females during breeding and non-breeding seasons. The data from individuals from all grids were combined as there were no significant differences by sex between grids for comparable periods. The cumulative mean home range area was determined by calculating the area for the first three captures, then adding the fourth capture and computing the new area, and so on (Haugen, 1942). These cumulative home range values of individuals were then averaged for each number of captures and plotted by season. The breeding males utilize larger areas than males in the non-breeding season and the females at all times of the year. Every animal was captured at least once, almost as many were captured twice or three times but very few were caught more than seven times. Thus, as the numbers of recaptures increase, the sample size on which each home range area mean was determined decreases and the reliability of that mean declines. This reduced reliability suggests that the curve may not reach the plateau phase as in the case of the breeding females.

2) <u>Distance moved between traps in 24 hours</u>

The average of the straight line distance that a mouse moved between traps on consecutive trap nights is shown in Fig. 3 which indicates that both sexes move more in the breeding season than they do in the non-breeding

Fig. 2   Cumulative home range area as a function of the
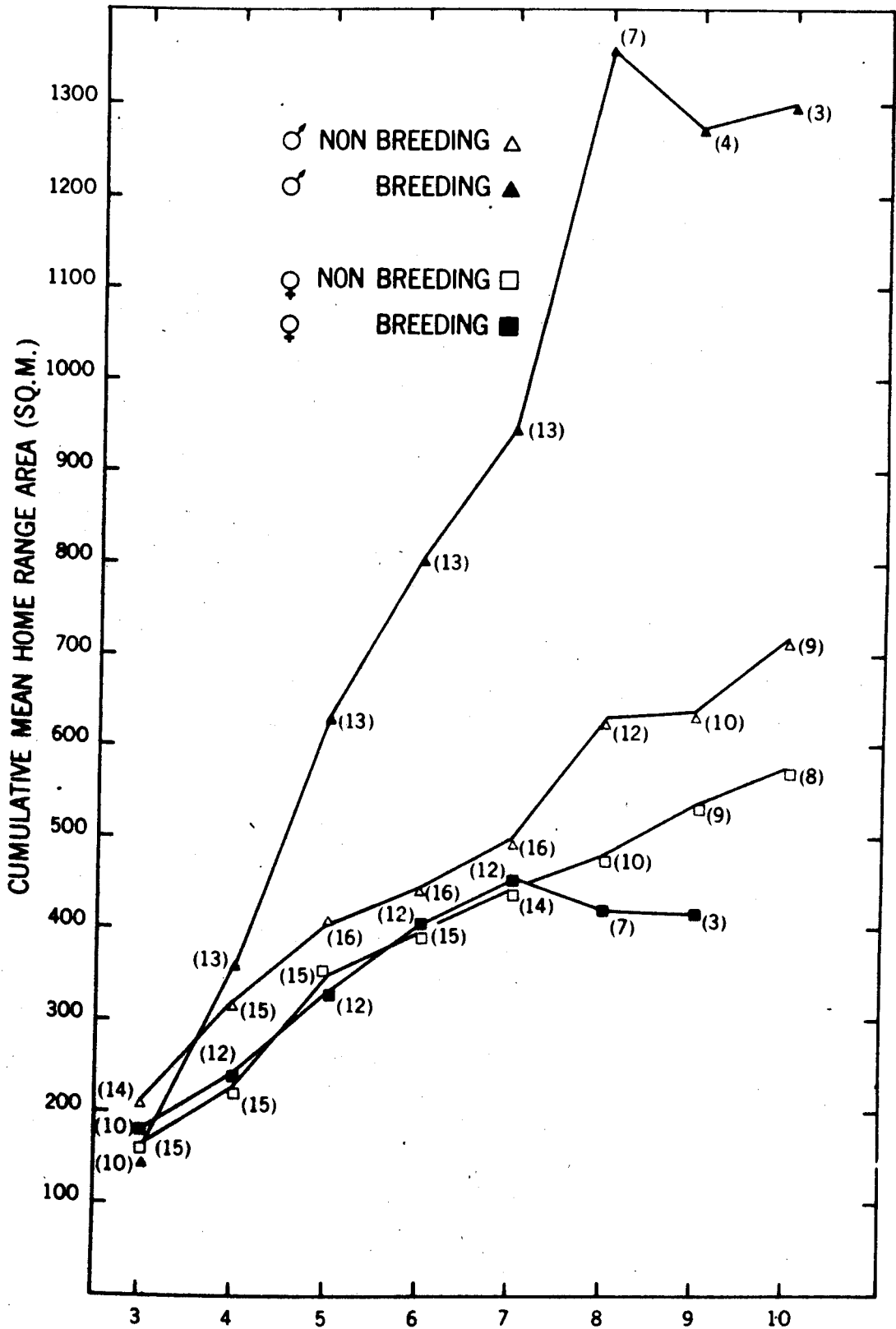
number of captures.

Fig. 3   Mean distances moved between traps in 24 hours

in different seasons.

MEAN DISTANCE (M.) MOVED IN 24 HOURS
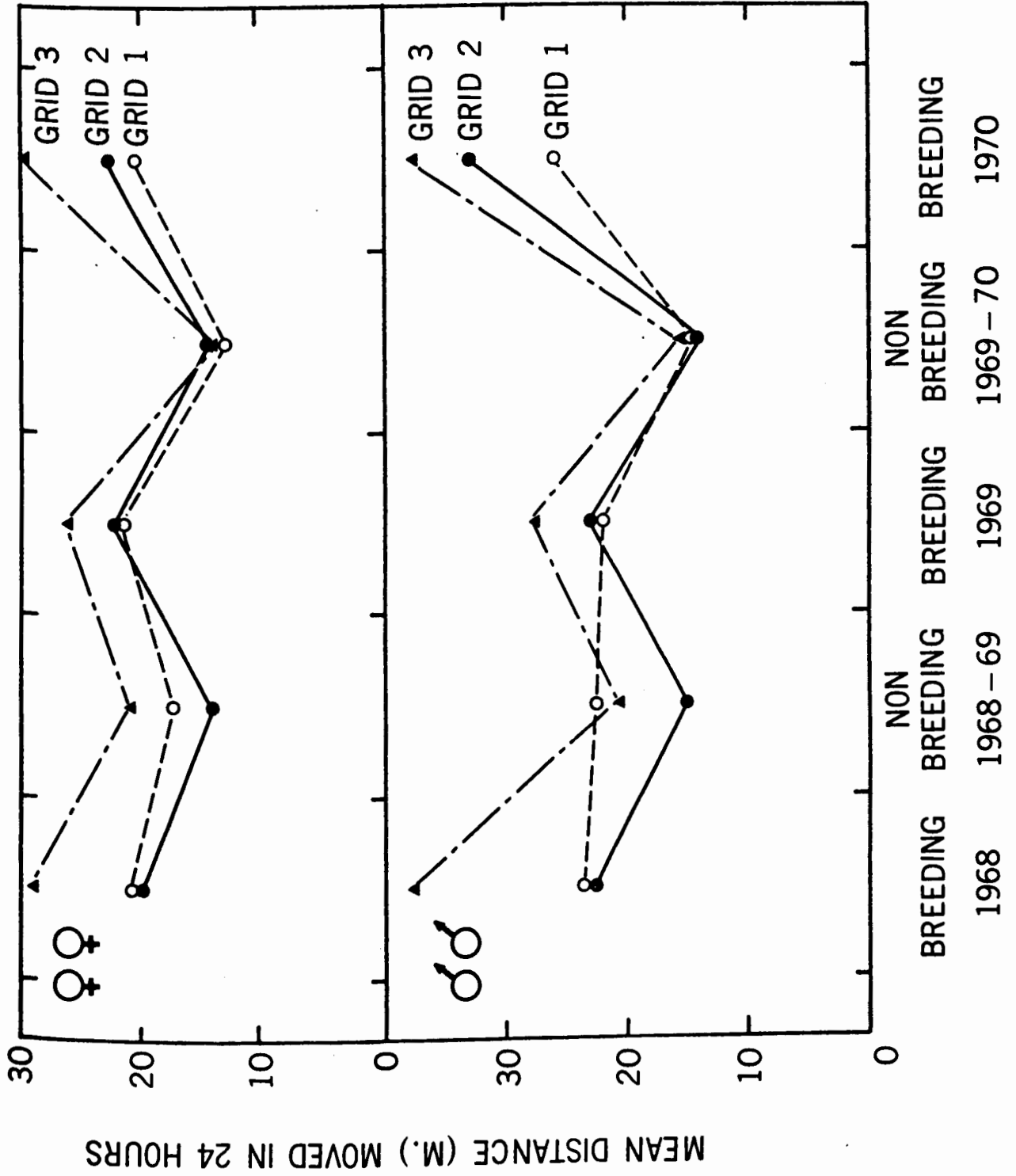
season. Males seem to move longer distances than females but the differences are not statistically significant (Students' "t" test, $p \leq 0.05$). The variability of this measurement did not make statistical comparisons possible but the pattern is consistent with shorter movements in non-breeding seasons on all grids and in both sexes. Also the minimum distance moved between smoked paper cartons in a single night suggested the same pattern of increased male movement in the breeding season (Table 1) although the differences were not significant. Females were not tested.

3) <u>Comparisons of home range determined by smoked paper and by trapping</u>

An attempt was made to determine the reliability of trap determined home ranges for male mice on Area 2, from January to September 1970. The areas of capture points from both the smoked paper and trap method were calculated separately using the minimum area method (Dalke and Sime, 1938). All capture points by both methods were then combined and used to determine the total area shown in the second column of table 2. Smoked paper area determinations (Justice, 1961) represent an average 82 percent of the total areas whereas trap area represents only a mean of 44.2 percent of the total area. These means are significantly different ($t = 3.544$, $p < 0.01$).

DISCUSSION

Although this present study was primarily concerned with the population dynamics of the species, <u>Peromyscus maniculatus</u>, it was hoped that some insight into its movements and home range activities might be gained from the trapping work. In this investigation home range size was determined by the

Table 1. Minimum distances moved by males between smoked paper

cartons in 24 hours.

MONTH		MEAN DISTANCE MOVED (M.)	NUMBER OF MOVEMENTS
Jan 1970	Non breeding season	38.0	(5)
Feb	Non breeding season	34.4	(8)
Mar	Non breeding season	–	–
Apr	Breeding season	45.5	(6)
May	Breeding season	45.3	(3)
June	Breeding season	65.8	(6)
July	Breeding season	50.7	(6)
August	Breeding season	28.0	(2)

Table 2. Comparison of home range area determinations based on trapping and smoked paper methods.

Individual male	Total Home Range Area (sq. m)	Trap-revealed Home Range (as percentage of total)	Smoked-paper revealed home range (as percentage of total)
#993	1795	67	81
#974	2350	62	100
#770	1150	26	100
#761	2050	29	85
#763	500	90	85
#695	600	33	67
#971	925	5	86
#969	800	25	81
#805	550	36	64
#581[1]	1250	16	42
#581[1]	1850	108[2]	65
#441	1400	33	107[2]
$\overline{X} \pm 1$ S.D.		44 $\pm$ 29	82 $\pm$ 18
Coefficient of Variation		0.66	0.22

[1] #581 was captured many times over a prolonged period and moved its home range during this time.

[2] These are artifacts due to the minimum area method measurement techniques.

minimum area method, although Brown (1962) and Van Vleck (1969) have
suggested that this method gives an underestimate of the total area. The
other methods of home range determination all involve mathematical manipulations
of basically the same data used in the minimum area calculations. Although
larger areas result from these techniques, they seem to offer no great
advantage over the minimum area method.

Haugen (1942) claimed that trap revealed home range increased rapidly
for the first few captures and then levelled off with further captures. The
number of minimum captures needed for an accurate estimate of total area is
where the slope becomes asymtotic (Haugen, 1942; Blair, 1951). I had hoped
to compare the home range size of deermice on the three study areas. As
Burt (1940) has stated, "the size of the area occupied by any animal is limited
by that animal's ability to travel and its necessity for food and protection".
Two problems arose which made such comparisons invalid. I attempted to compare
the mean home range sizes on different grids at comparable capture intervals
(i.e. mean home range size of males on grid 1 which had been captured 4 times
cf. mean home range size of males on grid 2 which had been captured 4 times)
but the variation in individual home ranges within a grid was so high that
comparison between grids was pointless. Because figure 2 never reached an
asymtote, I could not determine the minimum numbers of captures necessary for
an accurate determination of an individuals home range. Although the home
range of females in the breeding season tended to increase less after seven
captures, the home range area of males in both seasons continued to
increase with increased captures and showed no signs of

levelling off. There are three possible explanations for this steady increase in home range area: (1) either the mice were not captured a sufficient number of times and thus had not yet reached the plateau phase presumed to be required for an accurate estimate; or (2) the trapping grid area was too small so that mice were captured over only a small portion of their actual range, or (3) the basic premise of stable home range size is incorrect.

As 55 of the 492 individual mice captured in this study were captured 7 or more times over periods extending up to 4 or more months, and were thus definite residents of the grid areas, it would seem that the first explanation is highly improbable. The second is also most unlikely as none of the frequently captured mice were ever trapped on special trap lines placed 10 and 20 meters outside the grid periphery (see next chapter). The only hypothesis remaining is that the basic premise of a stable home range is not correct.

Burt (1943) defined home range as "that area around the established home which is traversed by the animal in its normal activities of food gathering, mating, and caring for the young. It excludes occasional sallies outside the area". Burt (1940, 1943, 1946) considered the home range of small mammals to be a well defined area which varies little in each individuals lifetime. My data, and that of Brown (1966) suggests that this is not correct. The concept of stability of home range areas

in small mammals has probably arisen due to the trapping regimes used. Most previous studies have been concerned with the population dynamics of a species over a short period of time, or during a certain defined period of the year. The home range in these cases was determined from a large number of capture points taken every night over 1 to 3 week period. Such intensive trapping would interfere with the movement of individuals especially in a trap prone species such as <u>P. austerus</u>, and give a biased estimation of home range size. In this study mice were only trapped for two nights (occasionally four) in each month. This resulted in a better determination of the area over which the mice were trapped during their entire life span as opposed to previous methods which concentrated on smaller periods of time.

The present study has produced some interesting data, which seems to be somewhat in opposition to current hypotheses explaining small mammal home ranges. Calculation of home ranges on the basis of captures in breeding and non-breeding seasons, showed that males covered considerably larger areas in the breeding season than do either males in the non-breeding season or females at any other time. This increased male movement during the breeding season (Fig. 2) could be related to a number of behavioural and physiological factors, for example males are more aggressive during the breeding season (Sadleir, 1965; Healey, 1967), which is probably an effect of increased testosterone production. It has been suggested

(Beeman, 1947; Scott and Fredericson, 1951) that increased levels

of testosterone cause male mice to become much more active. This

increased movement of male mice could therefore be attributed to

physiological changes associated with breeding. By moving over larger

areas, the probability of intercepting receptive females would

increase. If Sadleir (1965) is correct in his hypothesis that

population maintenance is based on agonistic behaviour of males towards

other males and juveniles, then, by roaming over larger areas in the breed-

ing season, the resident male mice could more effectively control the

number of competitors in an area. Both the trap and smoked paper records

(Fig. 3, Table 1) suggest that mice move greater distances between traps

or smoked paper cartons in the breeding season than they do in the non-

breeding season but this cannot be shown statistically. Krebs (1966) has used

such movement data to define home range size. In this study the mice on

Area 3 in the breeding seasons may possibly have had slightly larger

home ranges than mice on the other areas which may have been related to

the low population numbers and hence reduced social pressures.

It has already been suggested that the minimum area determination

for home range size is an underestimate. It was possible in this study

to compare the home range determination by two methods which showed that

the best estimate of actual home range size is probably the combined trap

and smoked paper sites. If this estimate is assumed to correspond to

100 percent of the actual range size then the smoked paper determination underestimated the total area by an average of 18.5 percent whereas the trap determined method underestimated it by 56 percent. Smoked paper was also useful in determining the total distance move by a particular mouse in a single night since there was no restrictions on its movement pattern. More importantly, although both methods are variable, over a series of animals (Table 2) the smoked paper method gave the least variable estimate of the total range area.

Thus, because the plateau phase was never reached, home range comparisons between areas were not possible. Hence the affects of environmental change on Peromyscus home areas could not be determined. What this study does suggest, however, is that Peromyscus may not have well defined areas and although the trapping system gives only a small number of records, the data indicates that P. maniculatus has a similar range shape and type to that described by Brown (1966) for A. sylvaticus whereby a central area is used intensively but there are occasional sallies outwards for a greater distance so that the home range resembles the hub and spokes of a wheel.

The populations of all species of _Peromyscus_, a cricetine rodent, are relatively stable. Many workers have demonstrated that these small mammals exhibit seasonal rises and decline in numbers but they are thought not to be cyclic, as are the microtines. Fuller (1969) suggested that _Peromyscus_ populations may cycle at Great Slave Lake, N.W.T. However, his study was carried out for only four years and the single peak in the numbers which he noted may not be an indication of a cycle but merely an aberration. In the Northern United States and Canada the common seasonal pattern is that of declining population numbers during winter and early spring because of the lack of reproductive activity during this time. The peak population occurs at the end of the breeding season (Blair, 1940; Howard, 1949; Orr-Ewing, 1950; Snyder, 1956; Tevis, 1956a; Sheppe, 1963; Davenport, 1964; Beer and MacLeod, 1965; Sadleir, 1965, 1970b; Terman, 1966; Harris, 1968; Fuller, 1969). Apparently the lack of reproduction during the winter months in the northern part of the United States and Canada can be attributed at least indirectly to the extremely low temperatures which prevail and Sadleir, Casperson and Harling (1973) have suggested that under these conditions caloric intake is insufficient to maintain pregnancy or lactation. Fuller (1969) has shown that delayed spring weather can adversely affect _P. maniculatus_ by causing delays in the spring weight increase and hence delayed sexual maturity - the ultimate effect being late first litters and consequently reduced recruitment of young into the population for that year, hence a decline in numbers. He attributes this decline in the population solely to environmental effects and not to population density dependent factors or to severe winter mortality.

Studies of the European field mouse, Apodemus sylvaticus, which occupies a niche similar to P. maniculatus, have shown a similar annual cycle, that is, declining numbers in winter and early spring; the peak occurring in late summer and early autumn (Miller, 1958; Kikkawa, 1964; Tanton, 1965, 1969; Ashby, 1967; Hansson, 1969; Watts, 1969). Tanton (1965) suggested that the low summer populations with increases in the fall, may not reflect true changes in numbers but rather a change in the behaviour towards the trap. He thinks that many individuals caught in the autumn are present in summer but for some reason do not enter the traps. A change in behaviour towards the traps, possibly related to a diminished food supply (Tanton pre-baited his traps for two days), results in more mice being caught in the autumn. This increase is due however to the recruitment of young into the population and not the appearance of old individuals present previously but uncaught (Ashby, 1962; Watts, 1966 - cited from Watts, 1969). Watts (1966) agrees with Sadleir (1965) that this increase of juveniles at the end of breeding is more likely due to better juvenile survival as a result of a change in the aggressive behaviour of the males.

Most studies of the population dynamics in Peromyscus have dealt with species that inhabit either old deciduous wood lots or grassland areas. Only little work has been done on Peromyscus in the rain forest of Western North America (Orr-Ewing, 1950; Sheppe, 1961; Sadleir, 1965, 1970b), although the deermouse is probably one of the most important mammalian omnivores in this ecosystem.

METHODS

Population Dynamics

(a) Field Techniques

From September 1968 through October 1970, three one hectare grids
(100 m x 100 m) previously described by Petticrew and Sadleir (1970;
see Appendix 1) were live trapped at four week intervals. The schedule
of trapping is shown in Table 3. In addition, grid 2 was live trapped
two weeks after each regular trapping from January through to September
1970. From June 1970 to August 1970, trap lines were set on the periphery
on Area 1 and Area 2. These peripheral lines were placed at 20 and 30 m
from the edge of the grid, so as to determine a crude estimate of emigration
from the grid areas.

The grids were marked out by labelled stakes at 10 m intervals. One
Longworth live trap was placed within 2 m of every stake so that a total of
121 traps were located on each grid (Plates 2, 3, 4). Traps contained
terylene batting as bedding and were baited with either whole oats, pelleted
rat rations or Purina mouse chow. The nest box portion of each trap was
enclosed in a cover of expanded polystyrene (Shaw and Milner, 1967) to
provide extra insulation for trapped animals. Traps were set on day 1
and checked in the mornings of day 2 and day 3. Traps were placed as
closely as possible to the same locations during each trapping period.

All deermice caught were weighed to the nearest 0.5 g using Salter
spring balances, sexed and ear tagged with serially numbered fish
fingerling tags. Their reproductive condition (Sadleir, 1970b) was also
noted. Testes size was determined by palpation and categorized as
large, medium, small, or undescended. Checks of snap-trapped individuals

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Table 3. Trapping schedule on each grid. The numbers in the
Table refer to week numbers with week 1 being the·
first week of June, 1967.

MONTHS	AREA 1	AREA 2	AREA 3	
1968				
October	73	71	72	Non-Breeding
November	-	77	77	Season
December	79	-	80	
1969				
January	87	84	-	
February	91	89	91	Breeding
March	95	93	95	Season
April	99	97	99	
May	103	101	103	
June	107	105	107	
July	111	111	111	
August	115	115	115	Non-Breeding
September	119	119	119	Season
October	123	123	123	
November	127	127	127	
December	131	131	131	
1970				
January	136	136	136	
February	140	140	140	
March	144	144	144	
April	148	148	148	Breeding
May	152	152	152	Season
May	156	156	156	
June	160	160	160	
July	164	164	164	
August	168	168	168	
September	172	172		
October	176	176		

(Week 1 was the first week of June 1967.)

Plate 2   General view of grid 1 photographed in

September 1970. Stakes marking the trap sites

can be seen in this and the subsequent two

plates.

Plate 3   General view of grid 2 photographed in

September 1970.

Plate 4   General view of grid 3 photographed in
                 September 1970.

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from other areas indicated that males with medium or large testes were
in reproductive condition because active spermatogenesis was noted in
the histological analysis. Males with small testes were either just
entering reproductive condition or regressing from it. Animals with
small or undescended testes were considered as non-reproductive. Female
reproductive condition was recorded as non-vascular or vascular, pregnant
or lactating. Females with vascular vaginae were found in the snap-trapped
samples to have cyclic ovaries, and were thus considered as potentially
reproductive.

Other mammals such as Sorex vagrans, Eutamius amoenus, Tamiasciurus
douglasi, Glaucomys sabrinus, Microtus oregoni (identified from Cowan
and Guiget, 1965) were recorded when captured. Since numerous Microtus
oregoni were trapped on Area 3, they were marked by toe-clipping,
weighed, sexed, and their reproductive condition noted. After January
1970 the numbers of M. oregoni dropped to a very low level and the marking
of individuals was discontinued. No voles were captured on this area after
June 1970.

(b) Analysis of data

Population parameters from multiple capture-recapture data can be
estimated by a variety of techniques. These techniques fall into two
broad categories, deterministic and stochastic. The deterministic models
assume that there is an exact survival rate over a specific time interval
(which usually equals the length of time between trapping periods), whereas
stochastic models estimate a probability of survival.

In the present study, Jolly's (1965) stochastic model was used
to analyse the data. This model uses all the information that is gained
from repeated recaptures, so that, despite the low numbers released at some
trapping periods, it is possible to give standard errors for the estimates
of the total population (N), probability of survival ($\emptyset$) and the number
of new animals entering the population (B) for each recapture period.
Jolly's model does, however, make some basic assumptions which are
difficult to test. The model assumes that: (a) sampling is random and
that marked animals have so redistributed themselves after release that
they have the same probability as any other animal of being caught in
subsequent trappings; (b) survival rates and probabilities of capture
are unaffected by the marking of animals; and (c) survival rates are
independent of the age of the animal. Although these assumptions are very
important for the absolute determination of the total numbers as well as
the other parameters in any one area, it should be noted that in this
study the model was used to compare populations on three areas. Therefore
provided that there are no differences in the validity of these assumptions
between areas, all comparisons of the population parameters are relevant
and valid.

In a summary of a variety of population estimation techniques,
Manly (1970) has shown that Jolly's method has a tendency to give a large
over-estimate when samples are small as well as a tendency to give pop-
ulation size estimates equal to the sample size. Despite Manly's criticism,

Jolly's model was considered to be an appropriate analysis method for this study, since an investigation of relative changes between areas formed the main part of this study and absolute changes in numbers were of secondary importance. Analysis was accomplished using a computer program written by Dr. C. Krebs of the University of British Columbia.

RESULTS

1) Seasonal fluctuations in numbers of males and females

Since each grid was one hectare in area all figures and diagrams dealing with numbers are expressed in terms of numbers per hectare. The monthly estimate of numbers for each area are shown in Table 4. Table 5 gives the correlation coefficients between the Jolly estimate and the minimum number of animals known to be alive at a specific point in time (t). It is possible for an animal not to be captured at time "t" but to have been caught at "t-1" and subsequently caught at "t+1". This animal is therefore considered to be alive at "t". Only 7% of such potential captures were missed. These correlates are significant in most cases indicating that both estimates are very similar. The 1968-69 winter was extremely cold with a heavy snow cover and during this time trapping was difficult. On Area 1, 11 of the marked males were caught in February which had not been caught in January. Their absence in that month resulted in an overestimate by the Jolly model. This probably accounted for the lack of correlation in numbers during the non-breeding period from October 1968 to the end of the breeding period in 1969. The single very high estimate of females by the Jolly model for January 1970 on Area 3 (Table 4)

Table 4. Comparison of estimates of total numbers (Jolly model and minimum number known to be alive)

MONTH	AREA 1				AREA 2				AREA 3			
	A		B		A		B		A		B	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
1968												
October	13	10	12	10	4	13	4	9	2	9	2	9
November	-	-	-	-	19	19	19	19	8	12	8	12
December	24	21	19	21	-	-	-	-	-	-	-	-
1969												
January	24	9	9	7	16	17	14	13	-	-	-	-
February	33	14	12	12	17	14	15	12	3	7	3	6
March	15	19	11	12	17	9	16	9	5	7	5	6
April	17	12	15	11	18	10	18	10	9	5	9	5
May	19	10	16	9	33	15	33	15	8	17	8	8
June	17	11	17	11	27	12	25	12	15	13	13	11
July	15	18	14	15	23	15	21	11	12	11	10	9
August	13	15	12	13	23	15	21	15	25	18	17	13
September	14	15	14	15	20	11	19	9	20	13	20	13
October	15	16	14	16	18	13	18	13	19	10	16	10
November	18	14	14	14	15	9	13	8	7	8	7	8
December	11	12	10	11	11	7	10	7	10	9	7	9
1970												
January	9	10	7	9	14	5	13	5	10	18	4	6
February	7	10	7	8	14	6	14	6	4	6	4	6
March	6	6	5	5	13	11	13	11	3	8	3	4
April	5	7	5	5	13	8	13	7	3	6	3	3
May	5	8	5	4	8	6	8	6	4	6	4	3
May	13	5	9	5	7	5	7	5	4	3	4	3
June	11	4	9	4	11	4	11	4	5	2	5	2
July	8	8	8	5	11	9	11	9	4	2	4	2
August	10	6	10	6	11	13	11	13			6	2
September	10	9	10	9	8	7	4	7				
October	9	15	9	9	16	13	16	13				
November			10	14			16	12				

A: Total number estimated by Jolly model (by sex).

B: Minimum number known to be alive (by trapping).

Table 5. Correlation coefficients comparing Jolly's N
estimate and minimum number known to be alive.

		AREA 1	AREA 2	AREA 3
Non-Breeding Season Oct-Jan	♂♂	0.225*	0.989	
	♀♀	0.991	0.953	
Breeding Season Feb-July	♂♂	-0.306*	0.989	0.988
	♀♀	0.788	0.763	0.725
Non-Breeding Season Aug-Mar	♂♂	0.953	0.978	0.927
	♀♀	0.979	0.977	0.448*
Breeding Season Apr-Oct	♂♂	0.857	0.934	1.00
	♀♀	0.746	0.994	0.801

* r is not significant.

which I cannot explain, but it had the effect of reducing the level of correlation of female numbers for the non-breeding period of 1969-70.

On Area 3 in 1969 both male and female numbers were low before breeding began and stayed low until mid-summer. Highest numbers occurred at the end of the breeding season, a pattern which has been reported by other authors, (Blair, 1940; Howard, 1949; Orr-Ewing, 1950; Tevis, 1950a; Sadleir, 1965, 1970b; Terman, 1966; Fuller, 1969). Area 2 follows the same pattern but the peak numbers occurred in the middle of the breeding season and not at the end. Area 1 did not show this trend, as female numbers stayed relatively stable although the males showed a definite decrease during this season. From the cessation of breeding in 1969 the numbers began to decrease, finally from the beginning of 1970, male and female numbers remained constant (Table 4). The only autumn increase was seen on Area 2 in October.

The Jolly model permits a reasonably accurate estimation of the mean number of animals present on an area over a number of sampling periods (Appendix 2). Table 6 gives mean numbers and variance by sex, area, and season and shows their statistical comparison. Because sampling periods were not coincident on all areas for each of the periods of this study, the best method of inter-area comparison involves using different groupings of monthly samples, so that the inter-area comparisons are coincident. Table 7 shows that the mean numbers on Area 1 and 2 were never significantly different whereas Area 3 had significantly lower numbers of males than Area 1 and 2 in three of the four periods; the females were significantly lower once. With the exception of the non-breeding period of 1969-70 the mean numbers on Area 3 were lower than on the other two areas.

Table 6. Mean Jolly N estimate (and variance) for all grids by sex and season.

	AREA 1 COMPARISON WITH AREA 2		AREA 1 COMPARISON WITH AREA 3		AREA 2 COMPARISON WITH AREA 3	
	AREA 1	AREA 2	AREA 1	AREA 3	AREA 2	AREA 3
Non-Breeding						
♂♂	19.97±23.29[x]	15.49±2.41	20.39±31.45[x]	5.47± 2.56	13.88±2.46	5.17± 2.56
♀♀	15.41± 2.55	17.35±4.73	14.45± 2.72	10.18± 1.01	16.61±4.11	10.21± 0.83
Breeding						
♂♂	19.05±14.88	23.25±4.53	19.62±17.80	8.79± 1.25	23.25±4.53	8.79± 1.29
♀♀	13.07± 4.77	12.18±3.32	14.16± 4.76	10.23± 7.62	12.18±3.32	10.23± 8.42
Non-Breeding						
♂♂	11.61± 4.35	15.91±5.00	11.61± 4.35	12.66± 5.83	15.91±5.00	12.66± 5.83
♀♀	12.36± 4.26	9.63±2.28	12.36± 4.27	11.67±10.11	9.63±2.28	11.67±10.11
Breeding						
♂♂	8.94± 2.23	10.56±1.94	8.50± 3.40	4.00± 0.90	10.00±1.79	4.00± 0.90
♀♀	7.68± 3.32	8.10±1.05	6.24± 3.65	3.80± 3.43	6.36±1.19	3.80± 3.43

[x]This pair of means, and others in the table, are not the same as sampling periods are not coincident. See explanation in text.

Table 7. Comparison of mean Jolly N values
between areas. (Test criteria values.)

		GRID 1		GRID 2	
		Males	Females	Males	Females
Grid 2					
Non-Breeding	1968/69	0.88	0.72	−	−
Breeding	1969	0.95	0.31	−	−
Non-Breeding	1969/70	1.41	1.07	−	−
Breeding	1970	0.79	0.20	−	−
Grid 3					
Non-Breeding	1968/69	2.56*	2.21*	3.89***	2.88**
Breeding	1969	2.48*	1.12	6.00***	0.57
Non-Breeding	1969/70	0.33	0.18	0.99	0.58
Breeding	1970	2.17*	0.92	3.66***	1.19

* = $P \leq 0.05$ ** = $P \leq 0.01$ *** = $P \leq 0.001$

2) <u>Seasonal fluctuations in total numbers</u>

The minimum numbers known to be alive for each month (both sexes combined) are shown for each area in Figs. 4, 5, 6. On all areas numbers were much higher in 1969 than in 1970. On Area 1 there was a dramatic increase in numbers in the second half of 1968, although the December 1968 peak was not maintained. From February 1969 onward there were usually twenty or more deermice per plot for the whole year and the numbers fluctuated little. However from October onward a persistent decline in numbers set in until March/May 1970. The numbers then increased until the end of the year but failed to approach the 1969 numbers.

On Area 2, the second half of 1968 showed a similar trend to Area 1. There was a similar mid-winter peak and a sudden decline and, with one exception, the numbers for each month through 1969 again stayed relatively constant although slightly higher than Area 1. The peak in May was due to a week-long trapping period which coincided with an exceptionally large number of juveniles dispersing through the area (see weight distribution, Fig. 10). Other week-long trapping sessions in January, February, March, and May 1970 failed to reveal any difference in numbers when compared to the normal two day trapping period. Area 2 differed from Area 1 in that early in 1970 numbers increased; although like Area 1, this was followed by a decrease to a May 1970 minimum. Thus, it can be seen that although the magnitudes are different, the numbers on Areas 1 and 2 fluctuate in a reasonably similar manner.

Fig. 4   Cohort diagram showing changes in numbers

and individual survival on grid 1.
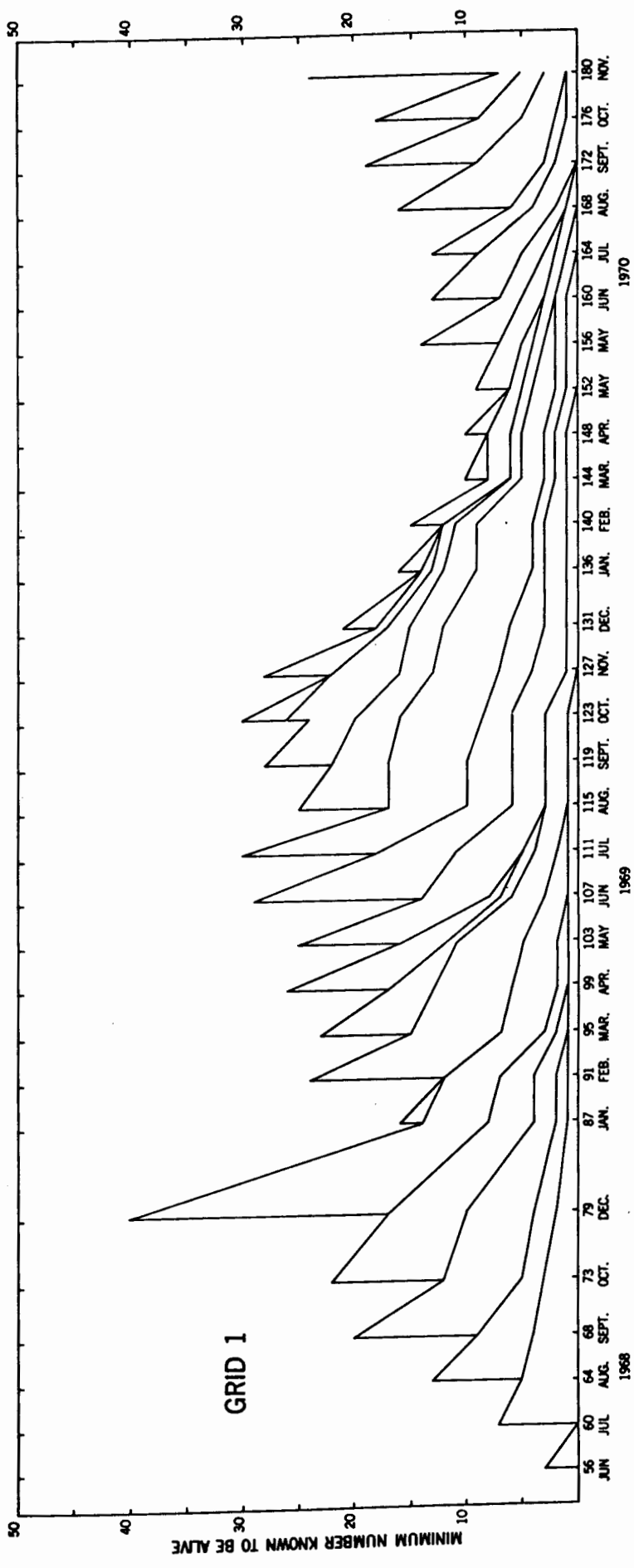
GRID 1

MINIMUM NUMBER KNOWN TO BE ALIVE

Fig. 5   Cohort diagram showing changes in numbers

and individual survival on grid 2.

GRID 2

MINIMUM NUMBER KNOWN TO BE ALIVE

Fig. 6   Cohort diagram showing changes in numbers and
                 individual survial on grid 3.

GRID 3

MINIMUM NUMBERS KNOWN TO BE ALIVE
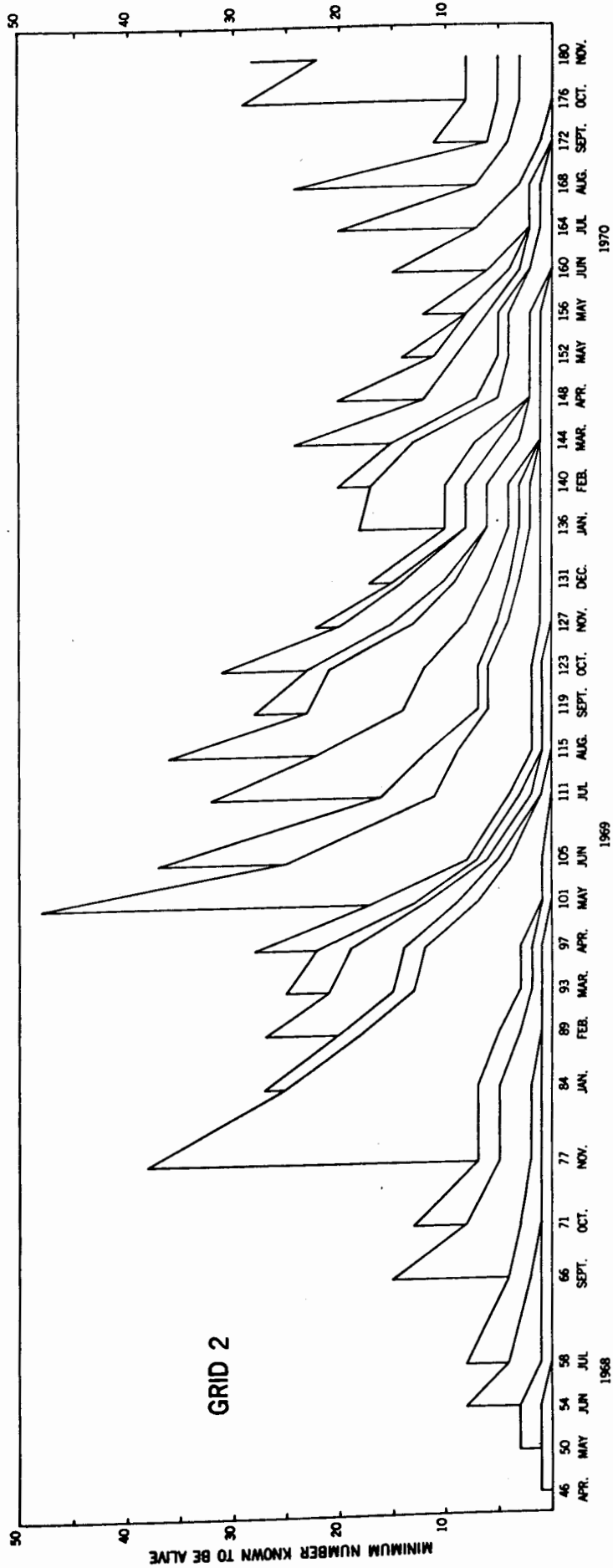
Area 3 (Fig. 6) showed a different pattern. Although there was a

similar increase in the second half of 1968, from January 1969 to September

1969 there was a persistent increase in numbers while the population highs

were maintained on Areas 1 and 2. There was, however, a decline from

September 1969 to March/May 1970 which paralleled that on other areas but

the population on this area showed no recovery and no mice were trapped

on it in August 1970. At this point trapping ceased on this area.

Table 8 shows that the total number of deermice for each month on

Areas 1, 2, and 3 are all significantly correlated for appropriately

comparable periods (Area 1/2 comparison is for 24 months while the

comparison of Areas 1/2 with 3 is for 21 months).

3) Probability of survival

Figs. 7 and 8 show that the probability of survival estimates

fluctuated considerably throughout this study. The degree of fluctuation

in monthly survival estimates of rodent populations has been reported

by many workers (Krebs, 1966; Sadleir, 1965; Tamarin and Malecha, 1971)

and is considered to be caused by many interacting small factors, analysis

of which would be extremely difficult. From Jolly's tables (see Appendix

3) an estimate of the mean probability of survival over several trapping

periods can be calculated along with its variance (Sadleir, 1965; see

Appendix 4). There is no difference at the 5% level, in the survival of

either sex of deermice between Area 1 and 2 and significance occurs only

between Areas 1 and 3 as well as 2 and 3 in the first non-breeding

period (Table 9). The significant difference may be an artifact due to

Table 8. Correlation coefficient comparing minimum
          numbers known to be alive on the three areas.

	MALES	FEMALES	COMBINED	N
Area 1 vs Area 2	0.68**	0.40*	0.61**	24
Area 1 vs Area 3	0.66**	0.80**	0.78**	21
Area 2 vs Area 3	0.54**	0.48*	0.60**	21

* $P \leq 0.05$ ** $P \leq 0.01$

Fig. 7   Males: Probability of survival ($\emptyset$),

recruitment (B) and Jolly's N

estimate for all grids by months.
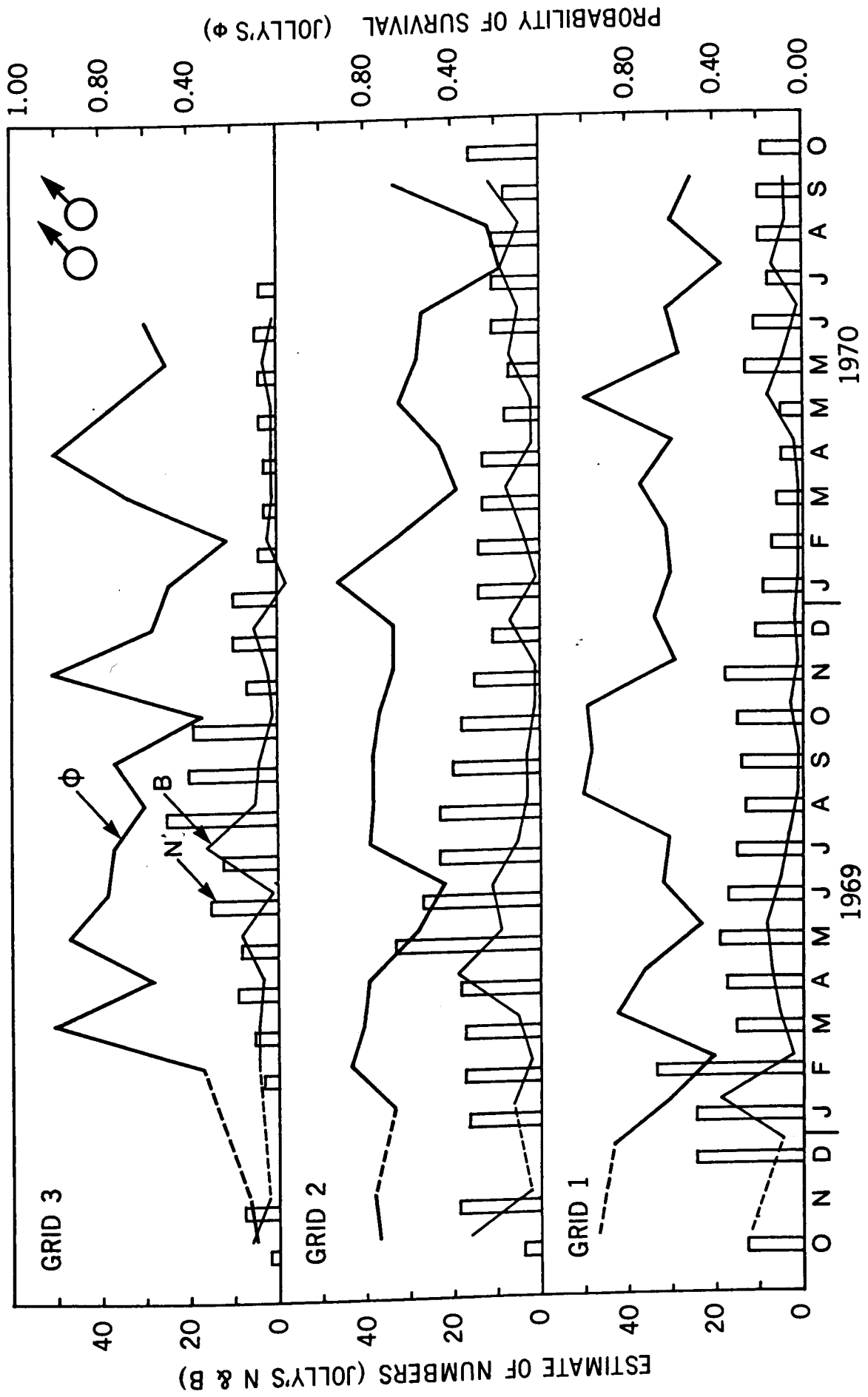
Fig. 8   Females: Probability of survival (∅),

                        recruitment (B) and Jolly's N

                        estimate for all grids by months.
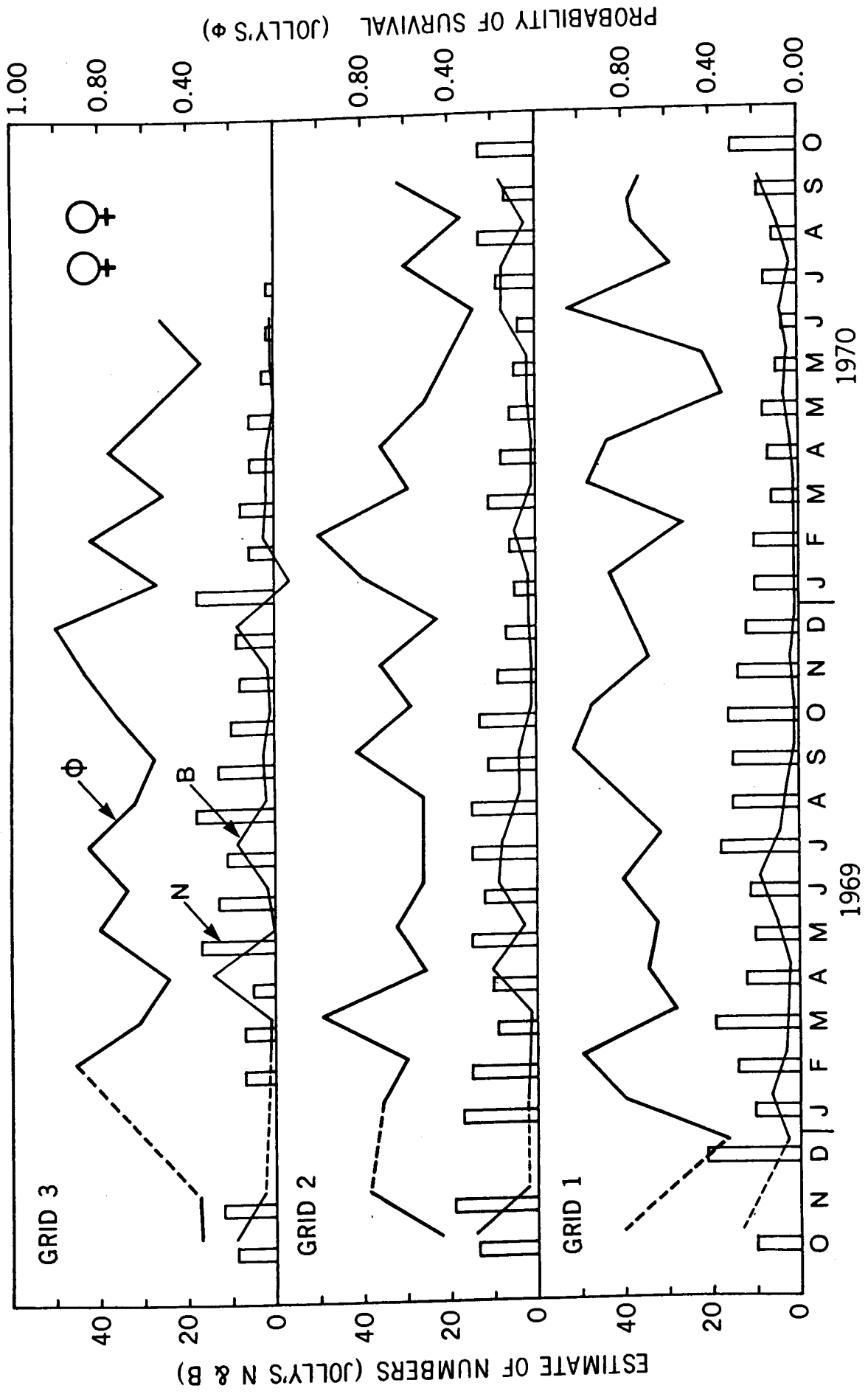
Table 9. Mean probability of survival (and variance)
for all grids by sex and season.

		AREA 1		AREA 2		AREA 3	
		ϕ	S^2	ϕ	S^2	ϕ	S^2
Non-Breeding Oct-Jan	♂♂	.322	.252	.744	.019	.189	.079
	♀♀	.637	.310	.644	.023	.181	.033
Breeding Feb-July (1969)	♂♂	.535	.017	.670	.009	.628	.058
	♀♀	.637	.026	.575	.019	.648	.048
Non-Breeding Aug-Mar	♂♂	.736	.023	.650	.011	.514	.044
	♀♀	.759	.023	.630	.018	.650	.068
Breeding Apr-Sept (1970)	♂♂	.536	.021	.379	.022	.684	.058
	♀♀	.547	.061	.398	.024	.501	.152

the small sample of two months for Area 3.   There were also no differences

in the survival of males and females on the same grids (P $\leq$ 0.05).

4) Recruitment   (Births and Immigration)

Recuitment generally increased during the breeding seasons as the

young of the year joined the population (see Fig. 7 and 8).   However,

between January and February 1969 there was an increase in the population

of Area 1.   This increase was directly related to a corresponding increase

in the recruitment.   The animals that joined the population at this time

were fully mature overwintered adults, as indicated by their body weight

(see Figs. 9, 10, 11).   A similar increase did not occur in 1970.   Area 2

followed a similar pattern to Area 1, although recruitment in the spring

of 1970 was higher than on Area 1.   The recruitment of both sexes during

breeding in 1969 was extremely high.   In 1970 an increase in adult

recruitment occurred from December 1969 to March 1970, but this adult

recruitment did not occur on Area 1.   Area 3 was much the same as Area 2

for 1969, but although there was an initial increase between December 1969

and January 1970, the adult recruitment on this area remained extremely

low for the remainder of this study.

5) Relative importance of recruitment, probability of survival, and

   length of season on change in numbers.

In order to determine the relative importance of recruitment,

probability of survival and length of season on changes in numbers these

factors were correlated with the changes in numbers seen for the six-

breeding and six non-breeding seasons. These correlations are shown in

Table 10. Changes in numbers were determined by subtracting the numbers

Fig. 9   Weight distribution on grid 1. In this and Figs.

10 and 11 the width of the polygram is proportional

to the frequency of individuals in each weight class.

Fig. 10   Weight distribution on grid 2.

Fig. 11   Weight distribution on grid 3.

Fig. 11   Weight distribution on grid 3.
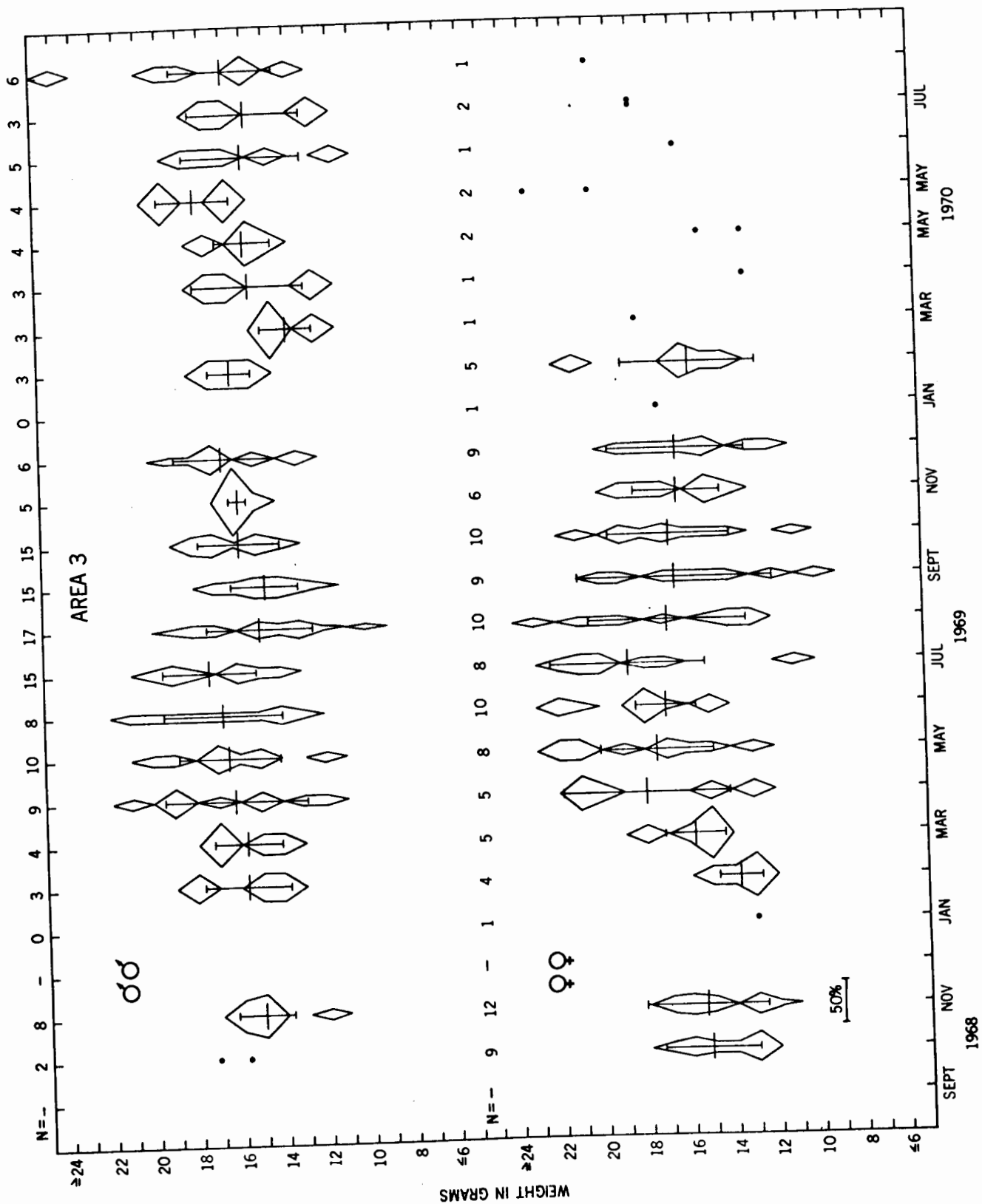
Table 10.   Correlation coefficients between male and female
            survival, total recruitment, length of season and
            changes in total numbers between the beginning and
            end of seasons.

	BREEDING SEASON	NON-BREEDING SEASON
Total Recruitment cf. Change in Total Numbers	.354	.817*
Total Recruitment cf. Change in Female Numbers	.480	.723
Total Recruitment cf. Change in Male Numbers	.180	.826*
Mean Female Probability of Survival cf. Change in Total Numbers	.185	-.401
Mean Female Probability of Survival cf. Change in Female Numbers	.083	-.575
Mean Male Probability of Survival cf. Change in Total Numbers	-.069	.043
Mean Male probability of Survival cf. Change in Male Numbers	.207	.143
Length of Season cf. Change in Total Numbers	.193 (.494)	-.936**
Length of Season cf. Change in Female Numbers	.0 (.837)	-.859*
Length of Season cf. Change in Male Numbers	.208 (.178	-.917*
Total Recruitment, Mean Female Probability of Survival and Length of Season cf. Change in Total Numbers	.714 (.536)	.946
Total Recruitment, Mean Male Probability of Survival and Length of Season cf. Change in Total Numbers	.756 (.780)	.963

( )   for 5 months on Area 3.

*   = $P \leq 0.05$

**   = $P \leq 0.01$

present in the last month of the season from the numbers present in the

first month. Total recruitment refers to the mean monthly recruitment

rates of both sexes combined. The disappearance of deermice from Area 3

presented problems in allocating a length to the breeding season in 1970.

Correlation coefficients for the observed season length of 5 months and

an assumed season length of 8 months, as occurred on areas 1 and 2, are

both given in Table 6 although survival and change in numbers could only

be calculated over 5 months.

6) Seasonal changes in body weight

　　　There is little variation in the mean weight by month of the adult

males on Area 1 during the study (Figs. 9, 10, 11). A single exception

was the increase in weight which occurred from January to March 1969.

Juvenile animals were considered to be any animals caught during or

immediately after the breeding season with a weight below 12 grams

(Sadleir, 1965). The most noticeable change in weight distribution occurred

during the breeding season, due to the numbers of juvenile males which

joined the population. The females on this area exhibited similar trends

as the males but with more variation in weight because of pregnancy.

After the breeding season had ended, weights for both males and females

tended to stabilize. It is also possible by looking at Figs. 9, 10, 11

to note the influx of juveniles into the population. Area 2 showed

similar trends to Area 1. Both males and females on Area 3 exhibited little

fluctuation in body weights, there being no gain in either sex at the

beginning of 1969. During the breeding period there was little variation

in weights indicating either that breeding success was very poor or that juveniles on this area were trap shy. There was one period of low body weights, August 1969, indicating juvenile recruitment.

7) Reproduction

On Area 1, males in both 1969 and 1970 came into breeding activity before the females (Table 11). In 1969 breeding commenced in late February but in 1970 it did not start until the beginning of April. Area 2 in 1969 exhibited much the same pattern as Area 1, although the males came into breeding condition a few weeks before the males on Area 1. The females on Area 2 came into breeding condition after male testes development had begun. In 1970 both sexes were in reproductive condition on Area 2 at the same time, this being synchronous with male condition on Area 1. Area 3 showed a trend in reproductive activity for both sexes which was similar to Area 1. Of the six breeding periods investigated it is interesting to note that in four (one instance being undetermined, i.e. Area 2 - 1970) the females remained in reproductive condition for at least one month after male reproductive activity had ceased.

8) Transients

Table 12 gives the number of resident animals as well as the number and proportion of transients caught per breeding and non-breeding period. There is no significant difference between grids in the proportion of transients which were caught (Chi square $P \leq 0.05$). Of the 126 deermice caught on the 20 and 30 m peripheral lines, 12 (10%) of these had been captured previously on the grid, whereas only 9 (7%) caught on the peripheral lines were caught subsequently on the grid.

Table 11. <u>Duration of breeding seasons on each grid.</u>

		GRID 1	GRID 2	GRID 3
1969	Testes descended	February (91)	February (89)	February (91)
	First pregnancy	March (95)	March (93)	March (95)
	Testes regressing	July (111)	July (111)	July (111)
	Last lactation	August (115)	July (111)	August (115)
1970	Testes descended	April (148)	April (148)	April (148)
	First pregnancy	May (152)	May (152)	May (152)
	Testes regressing	October (176)	August (168)[1]	[2]
	Last lactation	October (176)	September (172)[1]	[2]

( ) Month of study, see Table 3.

[1] See text.

[2] Sampling ceased in August when males and females breeding.

Table 12. Numbers of transient deermice on each grid by sex
and season.

		Area 1		Area 2		Area 3		TOTALS Area 1	Area 2	Area 3
		♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	1	2	3
1968-69 Non-Breeding Oct-Jan	Transients	8	12	·9	9	6	11	20	18	17
	Residents	12	13	11	16	3	8	25	27	11
1969 Breeding Feb-July	Transients	12	10	18	11	6	5	22	29	11
	Residents	28	12	48	23	16	15	40	71	21
1969-70 Non-Breeding Aug-Mar	Transients	2	6	3	13	11	9	8	16	20
	Residents	16	16	31	19	20	12	32	50	32
1970 Breeding Apr-Sept	Transients	9	10	23	20	1	2	19	43	3
	Resident	18	10	22	18	7	2	28	40	9

9) <u>Species composition</u>

From Table 13, it can be seen that the most frequently captured species was <u>Peromyscus maniculatus</u>. The interesting comparisons between areas reflect the vegetational successional stages. Area 3's most plentiful species was <u>Microtus oregoni</u>, the numbers of which are plotted on Fig. 6, indicating that this area contained a wide variety of grasses and other annual plants (Kellman, 1969) which make up a high proportion of the herbivorous voles diet (Lobue and Darnell, 1959).

DISCUSSION

This study investigated the effects of environmental changes on populations of deermice in a coastal forest. The general hypothesis was that differences in numbers, survival, length of breeding and non-breeding seasons would exist between the three areas studied. In addition, it was hoped that a population model could be developed to which all three populations would conform. Although there have been many studies on the biology of deermice, perusal of the chapter by Terman (1968) will indicate that there are very few studies which are sufficiently detailed. In addition, the majority of these studies which have been done, have been carried out on single trapping areas so that no analysis of between area comparisons were possible. Sadleir (1965, 1970b) attempted to trap several grids in adjacent areas but his grids were very small. In this study, it was hoped that the trapping schedule would give substantial data on variations between areas so that population changes over a large area could be considered.

Table 13.   Frequency of captures of all species
on each grid.

	AREA 1	AREA 2	AREA 3
Peromyscus maniculatus (deermice)	485	619	323
Microtus oregoni (vole)	24	13	450
Sorex vagrans (shrew)	93	140	34
Eutamius amoenus (chipmunk)	11	23	56
Tamiasciurus douglasi (squirrel)	1	0	0
Glaucomys sabrinus (flying squirrel)	3	0	0
Neurotrichus gibbsi (shrew mole)	14	29	1
Clethrionomys gapperi (Red-backed vole)	1	3	0
Zapus trimicronatus (jumping mouse)	0	3	0
Mustela erminea (weasel)	2	0	0
Slug	46	65	26

Maintenance of all populations at stable levels depends upon both intrinsic and extrinsic factors. The significance of such parameters and their interaction is difficult to assess. However, this study attempted to determine the relative importance of population parameters contributing to absolute numbers and their fluctuations. The discussion which follows will consider changes in the recruitment rates and survival probabilities in breeding and non-breeding seasons, in conjunction with the effects of various environmental conditions. The effects of these parameters will be discussed first separately and then as combined units.

The factors controlling the start of the breeding season in Peromyscus maniculatus have not as yet been fully determined. Whitaker (1940) has stated that for P. leucopus breeding is under photoperiodic control but his evidence is not very clear. In this study, breeding commenced in different months in different years which would suggest that photoperiod alone is not the major determinant. Sadleir et al. (1973) considered that breeding in wild deermice is strongly affected by the interaction of temperature and food supply acting through the energetics of activity and lactation. Thus, although there are considerable differences in the duration and onset of breeding seasons between years, in any population, the exact causes of these differences are not proven.

Population changes during breeding season

Recruitment during the breeding season is a function of the number of young produced and their survival. The number of young produced depends on litter size and the number of pregnancies in the population during the season. This is, in turn, dependent on the number of females which

reach sexual maturity during the season and the number which were originally available for breeding at the beginning of the season. The latter is directly related to the length of the non-breeding season as will be discussed later.

Recruitment during the breeding seasons was good, ranging from eight to fourteen new recruits per month. The single exception was Area 3 in 1970. On this area, the number of males and females was extremely low. As this period of low numbers coincided with a period of low survival in May-June, there was a further reduction in the potential breeding population. Also with the low number of females on the area the probability of male-female interaction was reduced. Survival probabilities fluctuated considerably and did not show any consistent trends between or within areas (Figs. 7 and 8). In the 1969 breeding season the mean survival probabilities were generally much better than those in 1970. Area 2, for 1970, showed a very low mean survival probability but still the total numbers on the grid increased (Table 9).

During the breeding season, the total population on the three areas increased with the exception of Area 3, 1970 which has already been discussed. In general, the probability of survival had considerably less effect on the population numbers than had recruitment even during periods of extremely low survival (Table 10). The increase of populations - during this time reflected more closely the recruitment of new mice in each area. Recruited mice may join either by being able to establish themselves in the hierarchial system, or by replacing overwintered mice that had died during the season, but the relative importance of these two

methods is not known. Also at the end of the breeding season, the social
system, i.e. hierarchy, begins to break down (Sadleir, 1965) with the
result that it is easier for recruits to establish themselves. In most
breeding seasons, recruitment more than compensates for the effects of
mortality and thus appears to be a more important parameter in the
breeding season than survival.

It would seem that the viability of a population from one year to
the next would depend, in part, on the number of mice present at the end
of breeding. Although Sadleir (1965) has suggested that aggressiveness
of dominant males plays a role in population regulation during breeding,
aggressiveness resulting in dispersal at the end of the breeding season
would not be advantageous, in terms of numerical consistency, to the
population, in terms of survival of that population in its particular
area. In this study, recruitment reaches a high point at or just prior
to the cessation of breeding. This is necessary to ensure that a large
number of animals are present at the onset of the non-breeding period.

Population changes during non-breeding season

The average level of recruitment for the two non-breeding seasons
were entirely different. Recruitment in the non-breeding season consists of
both adult immigrants or juveniles born in the previous season which join
the population. In 1968-69 recruitment on all areas was extremely high
(8 - 18 mice/month) and was probably due to both the long breeding
season which was 8 months and to the good survival of the previous genera-
tion. The large recruitment of 25 animals on Area 1 in January 1969
cannot be explained. In 1968-69 there was thus a large number of sub-

adult mice on all grids (Figs. 9, 10, 11). However, in 1969-70 recruitment

rates were stable and low, with only a few mature adult mice joining

the population. The monthly average of the probability of survival for

both non-breeding seasons, with the exception of Area 3, 1968-69 (where

the sample size was very small) was extremely high. For both sexes ϕ

ranged from 0.514 to 0.822 and was generally above 0.630 (Figs. 7 and 8).

In 1969-70 all areas showed a decline in the total numbers despite

good survival, which indicates that low recruitment was an important

factor (Table 4). In the previous year, 1968-69, increased recruitment

resulted in an increase in total numbers. The decrease in numbers in

the non-breeding season is much more noticeable in periods where the

season is long, as in 1969-70 (8 months). The mortality over a long

period of time, accompanied with low recruitment, resulted in a gradual

decrease in population numbers.

Other factors

Factors which may have also affected the population numbers on the

three areas include weather, parasitism, predation and disease. The

effects of these four factors were extremely subtle and consequently changes

in numbers as a result of these elements were difficult to assess.

Weather: The two winters were entirely different: the 1968-69 winter

was extremely cold, however, there was approximately 0.75 metres of snow

on the ground from late December to early February. This snow layer acts

as insulation, hence the ambient temperature below the snow did not

fluctuate much from 0°C. In 1969-70 the winter was relatively free

of snow but temperatures were below freezing, ranging from -10° to -5°C,

from mid-January to mid-March, the ground layers being frozen for most

of this period. In general, the monthly mean air temperature was the same

as the 9" (20 cm) soil temperature with the exceptions of periods when

snow was present on the ground. In this case the temperature under the

snow level ranged from -1° to 0°C (Harling, 1972) and hence

was considerably warmer than the mean monthly air temperature. In 1970

it would seem that mice which ventured out of their burrows would have

to use up all of their energy supplies to maintain themselves and would have

no surplus calories for the development of reproductive organs - the result

being that breeding started later. The opposite situation was true in

1968-69. This is reflected in the body weights of the mice during these

two comparable periods. The average weights of both male and female

mice at the beginning of 1969 was much higher than those in 1970, the

mice in 1969 also tended to show a rapid increase in weight. It is not

known whether this weight increase had any effect on the earlier

commencement of breeding in 1969 as compared to 1970.

Parasitism: Peromyscus carries a number of external parasites

(reviewed by Whitaker (1968)). The most predominant parasite, in this

study area, was the botfly, Cuterebra grisea. Hunter, Sadleir and

Webster (1972) have shown that there was no significant difference between

the survival rates of mice infected with C. grisea and those not infected.

Predation and disease: The effect of these two factors was very

difficult to assess.   Although such potential predators as racoons

(Procyon lotor), weasels (Mustela erminia), and owls were known to inhabit

all study areas, their combined effect on the population was not known.

There were however, no sudden dramatic declines in population numbers

during the study, such as result after intensive predation.   With

regards to disease, the dead sample study gave no indication of any major

disease outbreak in the mouse population (Casperson and Harling, personal

communication, 1972).   Occasionally some mice had abnormally large and

discoloured lungs and liver indicating an unidentified infection.   Again

the effects of this on the population was not known.

Population models

From the preceding information it is possible to deduce a generalized

scheme of events which is consistent with the fluctuations of all three

populations of deermice.   The most important factors affecting the changes

in numbers are recruitment and the length of the non-breeding season (Table

10).   It is this change in numbers which governs the numbers of potentially

breeding deermice which are present at the beginning of the subsequent

reproductive season.   The significant negative correlations in Table 10

show that if the non-breeding season is short, populations of deermice

are dense at the beginning of the subsequent breeding season.   If the

non-breeding season is long, the numbers entering the breeding season are

reduced and do not increase with such a season until it is well progressed.

There are, therefore, four possible model proposals, assuming that the

rate of recruitment is at its highest point after the cessation of breeding

and then steadily declines as the non-breeding season progresses (i.e. the recruitment curve is skewed to the left). The four possibilities are: 1) short non-breeding season with a high average recruitment; 2) short non-breeding season with a low average recruitment; 3) long non-breeding season with a high average recruitment and 4) long non-breeding season with a low average recruitment. Mortality or its converse, survival, does not appear to be an important factor affecting the change in numbers (Table 10). Of the four possibilities, 2 and 3 are unlikely on the following grounds:- possibility 2 could only occur if the prior breeding season had a very low recruitment and/or poor survival. Possibility 3 is extremely unlikely as this requires continual recruitment on to the area throughout the long non-breeding season. As the majority of recruits to any area are juveniles from the previous breeding season it would be impossible to maintain a high average recruitment through the seasons. The remaining two possibilities 1 and 4 were both observed during this study. Possibility 1 occurred in the non-breeding season of 1968-69. This involved a short four month season with high average monthly recruitment (10 to 18.3 mice/month). Trapping by Casperson (personal communication, 1972) revealed a similar pattern on grids 1 and 2 for 1970-71. Possibility 4 occurred in 1969-70 when the season was eight months long and average monthly recruitment was low (2.8 to 6 mice/month). During the breeding season the relationship between the change in numbers and the number of males and females present differed. The low correlations using an eight month season on grid 3 (1970) were almost certainly an artifact as the actual

change numbers, for each sex, could not be determined since the population vanished. However, when the correlations were determined on the observed data, 5 months in duration, the r value was much higher for females than males and was statistically significant. Therefore it appears that, during the breeding season, the change in the number of males is relatively independent of the length of the season. This concurs with the suggestion of Sadleir (1965) and Healey (1971) and the observations of Fordham (1971) that the numbers of males during breeding seasons remain fairly constant and are probably determined by the level of their agonistic interaction.

It is now possible to propose a general model for the regulation of numbers in this species. During breeding seasons the numbers of males appears to be regulated by their agonistic behaviour toward each other. The males are aggressive to all juveniles but those females which do reach sub-adulthood are tolerated and hence the numbers of females can increase as the season progresses. During the non-breeding season the regulation system changes and individuals of both sexes regardless of age appear to act in a similar fashion. Although recruitment rates are low at this time, change in numbers is more correlated with recruitment during the non-breeding season than during the breeding season. However the strongest correlations are with the length of the non-breeding season. If the non-breeding season is short, numbers change very little and pop- ulations remain high and are relatively dense when breeding commences. If the non-breeding season is long, there is a steady decrease in numbers as the monthly mortality operates over an increasing period of time. When breeding commences after such a period, numbers are extremely low for

the first part of the season, showing an increase only at the end of the season. In summary, to use an analogy the "capital" present during the breeding season is mainly a function of the size of the initial "deposit" and much less a function of the seasons "interest" or "withdrawals". In turn the "deposit" is controlled by the length of the previous non-breeding season.

CHAPTER 4

BEHAVIOUR - INTRODUCTION

The seasonal incidence of aggressive behaviour and its correlation with

testes condition has been reported for a variety of rodents and other

species (Beeman, 1947; Davis, 1964; Scott and Fredericson, 1951). Davis

(1963) correlated an increase in territorial behaviour with an increase

in the size of gonads in birds, and noted that injections of androgens

in domestic fowl (Gallus gallus) resulted in fighting and courtship.

He concluded that androgen levels controlled such behaviour. Beeman (1947)

showed that testosterone levels affect aggressiveness in white mice

(Mus musculus) whereas McCabe and Blanchard (1950) demonstrated that

the intensity of fighting in Peromyscus californicus and P. maniculatus

varies with the season and testes weight. Levy and King (1953) injected

immature rodents with testosterone and noted increases in aggressive

behaviour with increased dosages of this hormone. Lagerspetz (1969)

reported that aggressive behaviour in M. musculus does not begin without

the presence of male hormones and a decrease in the androgen level results

in a decrease in aggressive behaviour. Whitaker (1940) suggested that

increases in day length stimulate testes development in deermice

with   an   increase in testosterone production release, and resulting in

a potentiality for increased aggressiveness. Female reproduction in

P. maniculatus is affected by photoperiod (Price, 1966).

Changes in agonistic behaviour of male deermice (P. maniculatus)

have been measured in connection with a field study of the species

population dynamics by observing the arena behaviour of individual field collected males towards strange laboratory males (Sadleir, 1965). Sadleir suggested that the survival of juvenile deermice is influenced by the aggressiveness of the adult males of the population. During the summer when adult aggression is high juvenile survival is poor, but in the fall when aggression decreases juveniles survive well. Healey (1967) has confirmed Sadleir's conclusions.

In both these investigations field animals were isolated from their social and natural environmental contact for extended periods of time. It has been found that even short periods of isolation can induce aggressive behaviour (Sigg, 1969). This suggests that the levels of aggression determined by Sadleir and Healey may have been too high, although it should not affect the seasonality of changes in behaviour. In addition both Sadleir and Healey tested their field animals against laboratory animals which had considerable experience of bouts in an arena.

This present study attempted to document seasonal and individual changes in male behaviour by: (a) testing field animals against each other (so that each opponent had approximately equal bout experience) and (b) by reducing as much as possible the length of isolation time of the tested males. In addition it was hoped that detailed studies of home range could be related to an individual's aggressive level.

METHODS

Behaviour Investigations

From January 1970 through to September 1970, all male deermice
captured on day 3 on grid 2 were taken to the laboratory to determine
their relative levels of aggressiveness. This was done every second week,
so that captured males were placed in a bout only once per two week
period. Female aggressive behaviour was not examined because of the
presumed complicating factors associated with pregnancy and estrus
(Sadleir, 1965).

Aggression between males was assessed by observing their behaviour
in a neutral arena measuring 24" x 12" x 12", with a vertically sliding
partition which divided it into two. One side of the arena consisted of
clear perspex through which observations could be made. Only two mice
were observed each time and no individual deermouse ever met another
individual more than once per bout per two weeks. Care was taken to
match animals from extreme ends of the grid to reduce the possibility of
prior contact between the opponents. Mice were first placed one on each
side of the partition for a period of five minutes. One of the mice was
marked with a coloured flowpen. After five minutes the partition was
lifted. Each matched bout was observed for five minutes and aggressive
encounters were described into a tape recorder. Most of the behavioural
units described by Eisenberg (1962) were noted, but only the aggressive
units, as summarized by Sadleir (1965), were recorded. These were as
follows: (1) jumping at an opponent; (2) chasing opponent; (3) threatening
opponent; (4) upright threat; (5) grooming of a defeated opponent,

(6) being groomed by a defeated opponent; (7) fighting. Upon completion

of a bout each encounter was transcribed from the tape recorder onto

data sheets. Each data sheet was subdivided into ten second intervals,

thus an aggressive unit was scored if it occurred within a ten second

interval. If more than one unit of the same type occurred within the ten

seconds it was scored only once but other units were scored within the

same time period if of a different type.

RESULTS

1) Sexual condition of mice used in behaviour tests

Since testes development is an important factor governing the agonistic

responses of male mice (Beeman, 1947), it was essential that the mice

tested were sexually representative of the population on the grid. Fig. 12

shows that this was the case. Tested mice and grid mice were not in

full breeding condition until the beginning of April and they ceased

breeding at the same time. During the latter part of this study several

juveniles were tested against resident adults which explains the presence

of mice with small testes in June and August.

2) Aggressive acts as a function of time

The average number of aggressive acts per bout for each month is

shown in Fig. 13. This figure also gives the total number of fights per

month. This seasonal aggressive cycle is similar to that suggested by

Sadleir (1965) and Healey (1967). Increase in aggression from February to

March is coincident with an increase in testes development (Fig. 12) suggest-

ing that there is a possible relationship between testosterone secretion

Fig. 12   Sexual condition of grid and tested males.

SEXUAL CONDITION – GRID MALES

SEXUAL CONDITION – BEHAVIOURALLY TESTED MALES

1970
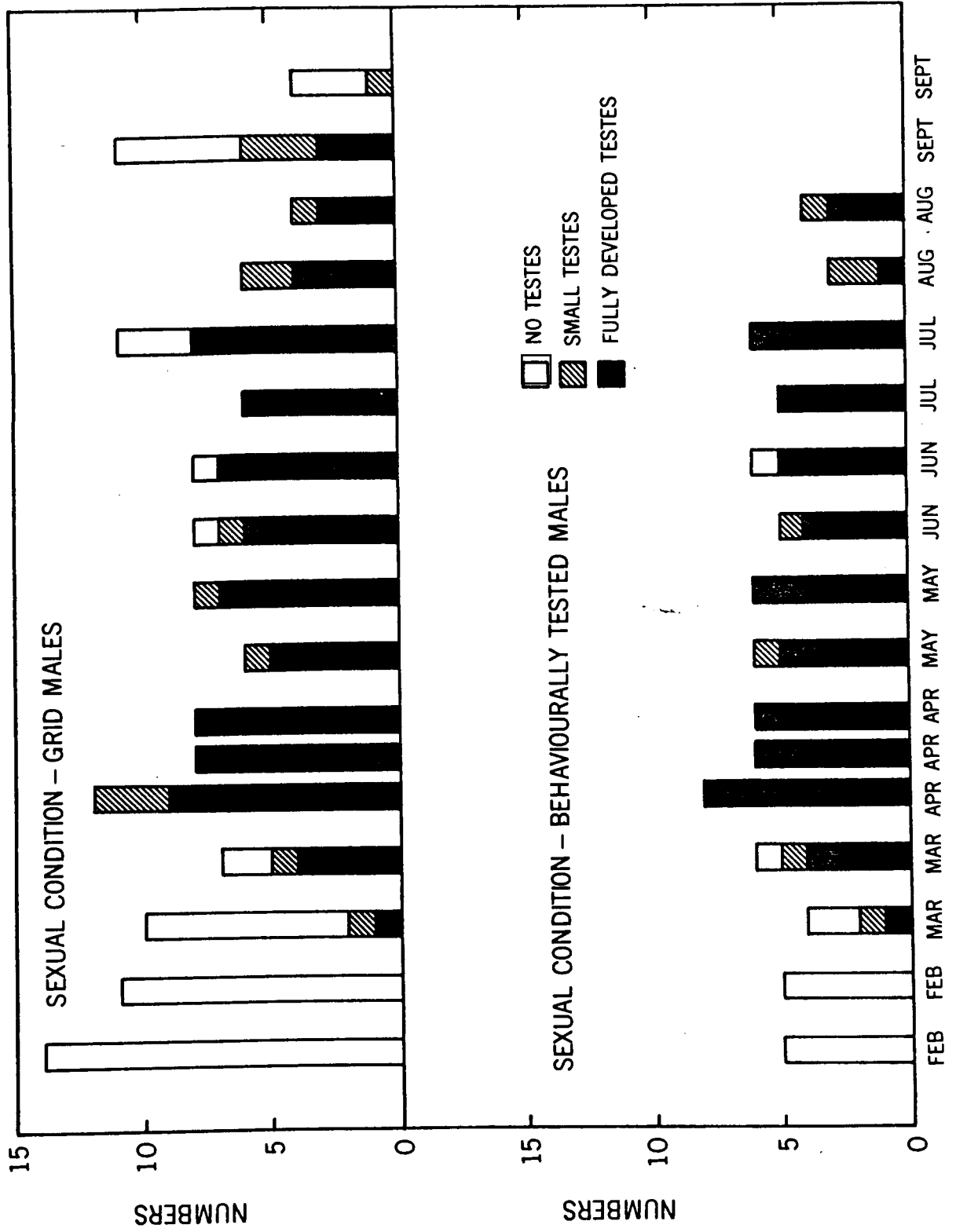
Fig. 13   Average number of aggressive acts per bout by

               months and number of fights.

NUMBER OF BOUTS WITH FIGHTS

MONTHLY AVERAGE OF THE NUMBER
OF AGGRESSIVE ACTS PER BOUT

NUMBER OF BOUTS
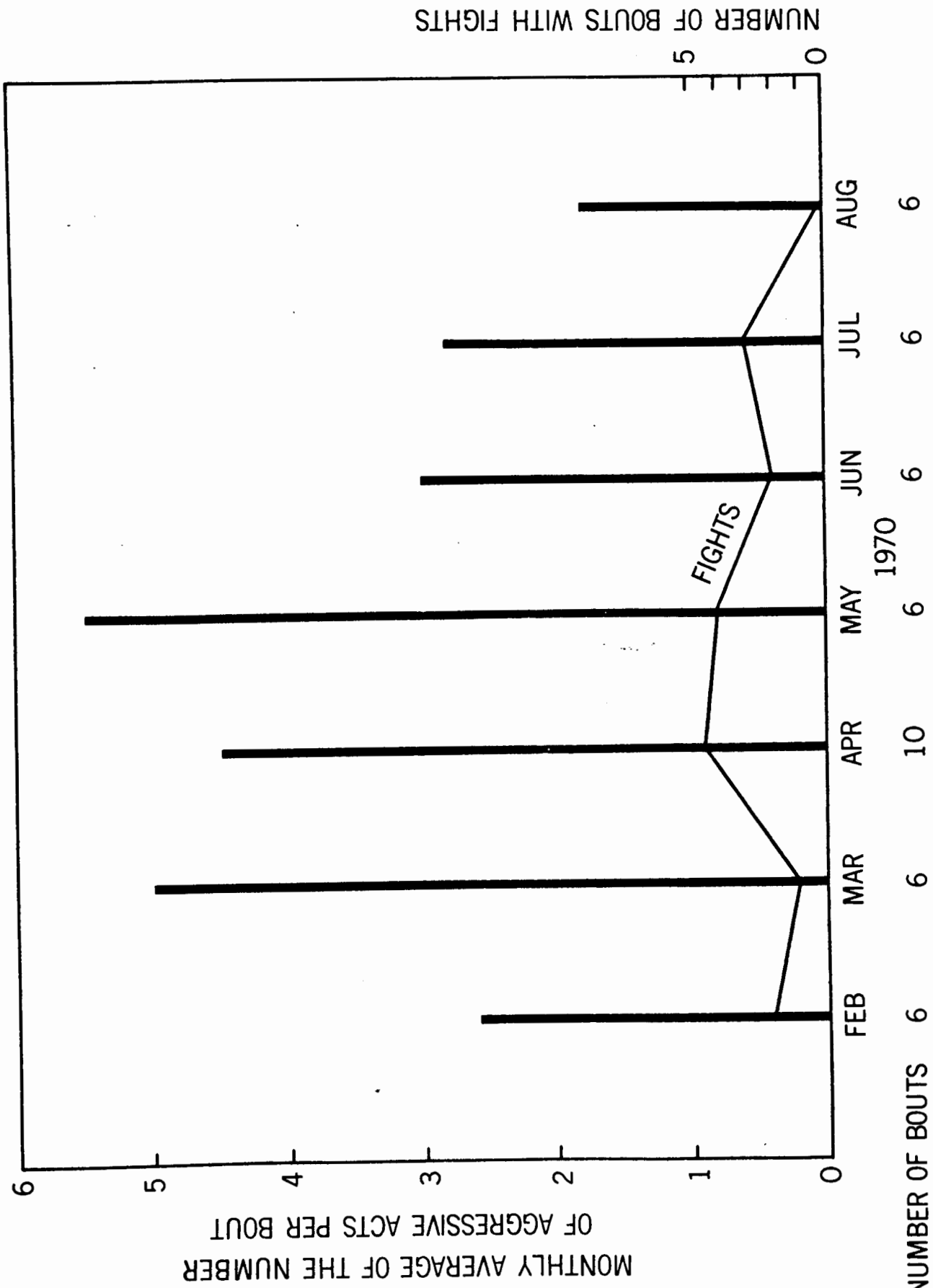
and aggression. However, the decrease in aggressive behaviour from May to June does not coincide with regression of the testes which occurred much later in August.

3) The relationship of aggressive behaviour to home range area.

Fig. 14 compares aggressiveness and home range area occupied for the six males which had participated in four or more bouts. Their hierarchial relationships were not clearly defined. Aggressive tests were conducted on a further 22 males but because they were tested less frequently, it proved difficult to determine their relative social status. However, it is likely that the relationship shown for the six males in Fig. 14 would have held for all adult males on the area. The scatter diagram indicates that there is a relationship between aggressiveness and area covered, and although the sample is small, the correlation coefficient (r = 0.804) achieves significance at the 10 percent level.

4) Inhibitory behaviour

During fights a submissive act was observed which totally inhibited further aggressive acts by the winning male. This act consisted of a short chirp or chit and was emitted when the submissive male was lying on its back and is similar to a behavioural act described by Eisenberg (1962). Of the 26 bouts where a decisive behavioural outcome could be determined (i.e. dominance of one male over the other), 19 of these bouts included a chit response from the submissive. In cases where juveniles were matched against adult mice the chit response did not have the same totally inhibitory action; the adults would continue to threaten and sometimes attack the juveniles, although the juveniles remained in a totally submissive posture.

DISCUSSION

Beeman (1947), Scott and Fredericson (1951) and Davis (1964) have
shown that agonistic behaviour in rodents is influenced by androgen
secretions. At the beginning of this study testes were not developed
and aggressive activity was minimal.   As the testes increased in size
at the beginning of the breeding season and became located in the scrotal
region, the number of aggressive acts increased. In the wild population
the proportion of males in sexual condition increased gradually as the
season progressed.   The trapping record of individual males
showed that their testes increased in size suddenly (Fig. 12).

Agonistic behaviour probably operates in the first part of the
breeding season by establishing an adult male hierarchy in the population.
This subsequently decides recruitment, dispersal, and thus indirectly the
size of the population. Fordham (1971) has shown that excess food placed
on an area causes considerable increase in the total population but
this increase is not reflected in an increase in the complement of resident
adult males. Brown   (1962) found that the adult male Apodemus sylvaticus
which were resident on the area at the commencement of breeding was
dominant and controlled the stability of the society. She stated that a
hierarchial system existed between these mice. The hierarchy is extremely
important since it defines the relationship of mice in a particular area
so that intruders are more readily identified. Sadleir (1970a) has shown
that hierarchial systems do exist for Peromyscus maniculatus austerus.

In this study it was difficult to determine the relationships of the adult males on the grid. Six mice were considered to be dominant and hence constituted a possible hierarchy. But there are two possible hierarchial systems, first the top six mice control the entire area and there exists no relationships between the mice which do not constitute this hierarchy, that is, the non-hierarchial mice are of equal status one to another. Or second, a continuum exists whereby the behavioural position of every male on the grid is defined and the status of one to another is very strictly regulated. Therefore, which system existed in this study was not determined because the frequency of testing and trapping made it difficult to define the status of non-hierarchial mice.

Death or emigration of any member of the hierarchy would result in competition for the vacant position and home range by juveniles and transient adult mice as well as "lower members" of the hierarchy. This leads to a socially unstable condition and a possible reduction in dispersal pressure until the re-establishment of a new social hierarchy. During this period it is possible that more mice could be supported on the area. Nowack (1971) reported that removal of the first and second dominant male <u>Mus</u> <u>musculus</u> caused an increase in aggressive acts indicating that the hierarchial relationships had been disturbed. She also demonstrated that there was a decrease in the number of fights through time and suggested that this can be explained by the establishing of orderly relations between individuals. The natural analogue to the behavioural action described by Nowack (1971) would be the death of a dominant. In Fig. 13 it can be seen that the

highest number of aggressive acts was in May. This coincided with the death of two of the hierarchial mice; also the number of fights was relatively high, indicating a possible change in the social structure of the population. However, this analysis of the effect of the death of two hierarchy mice is complicated by influxes of juveniles in May. Therefore, it is difficult to determine which social change caused the increase in aggressive acts and fights.

The pattern of aggressive acts (Fig. 13) follows very closely that described by Sadleir (1965) and Healey (1967). The peak in May coincides with the first influx of juveniles. The survival of juveniles is related to adult male aggressiveness as adult females do not take part in any of these behavioural interactions (Healey, 1967). The response of adult males matched against themselves as opposed to those matched against juveniles was entirely different (see section 4 of the results). In the first place when an adult male was in a submissive position and the dominant continued to attack, the submissive would emit a chit which completely inhibited further actions by the dominant. However, when an adult male attacked a juvenile and the juvenile emitted a chit, the adult male was generally not inhibited and continued to attack or threaten the juvenile. This would suggest that the adult males are more persistent in their aggressiveness to juveniles which would act to ensure their expulsion from the home ranges of such males. This agrees with the hypothesis of Sadleir (1965).

The relationship between home range or territory and aggressive-
ness has been demonstrated for prairie gophers (Cynomys ludovicianus)
by King (1955), woodchucks (Marmota monax monax) by Bronson (1963), and
for red grouse (Lagopus lagopus) by Watson (1964). In all these studies
the animal concerned was easily observable in a natural situation. This
study has also shown that a similar relationship possibly exists for
P. m. austerus and it was possible to deduce such a correlation from
field studies, despite the complexity of the environment and the species'
nocturnal habits (Fig. 14). The biological reasons for the existence of
such a relationship for this species are difficult to determine. One
possible advantage would be the unhindered movement (i.e. few behavioural
interactions with other adult males that may be encountered) over large
areas, thus increasing the probability of encountering more females or
better food supplies. Whether the home range areas of the top hierarchial
mice are related to food quality or quantity or optimum habitat suitability
is not known.

CHAPTER 5

FORESTRY IMPLICATIONS

The role of Peromyscus as a seed eater and its relation to reforesta-
tion programs by direct reseeding has been well documented (Kverno, 1954;

Shaw, 1954; Spencer, 1954; Ahlgren, 1966). Shaw (1954) claims that a

deermouse can consume as many as 200 Douglas fir (Pseudotsuga menziesii)

seeds a day even when alternate food is available. Tevis (1956a) and

Ahlgren (1966) have noted that the populations of Peromyscus increase

after logging operations. This increase is associated not only with

seeds as a food source, but also with the presence of large quantities of

insects in the burned slash areas and areas where vegetation is recovering.

The increased presence of seeds is a function of the destruction of the

"A" soil horizon layer by fire or erosion and consequently the increased

availability of seeds (Spencer, 1954). The use of rodenticides as a

control method has proven to be unsatisfactory, since, as Spencer (1954)

has pointed out, although 95% of resident populations can be controlled,

as few as six deermice per acre can nullify a program in which treated

Douglas fir seed is broadcast at the rate of one-fourth pound per acre.

The failure of direct reseeding has forced the forest industries to rely

heavily on the age old method of growing seedlings and planting them by

hand, but the advance in labour and material costs in recent years is

creating renewed interest in direct reseeding.

The two previous chapters have discussed the population dynamics, and home range in three different forest regimes of P. maniculatus. These previous chapters have shown that there are: (1) probably no differences in home range patterns or movement activities between any of the three populations (Fig. 3); (2) no differences in the probability of survival of either sex on the same area or between the three areas (Table 9); (3) no differences in recruitment (Figs. 7 and 8); and (4) there did exist, however, differences between grids 1 and 3, and 2 and 3 in the number of mice supported per hectare, grids 1 and 2 generally supporting more mice than grid 3. The aim of this chapter is to discuss previous results in relation to forestry practice. In addition, it was hoped to relate the knowledge gained to the practical aspects of a reforestation program. This could be done by recommending an optimum time for aerial reseeding to be conducted in relation in the annual cycle of P. m. austerus or an ideal time for various types of control methods to be implemented.

The numbers of deermice on all three grids seems to be related to the successional stages of the logged areas. Diebold (1938) has suggested how logging operations could possibly effect rodent populations. He stated that the removal of stands of coniferous trees tends to allow winter snowfall to accumulate on the ground and act as an added insulating layer that prevents the soil from freezing. In thick conifer stands, the tree crowns tend to intercept the snow which then evaporates or melts and drips to the ground where it freezes. Frozen soil would prohibit Peromyscus maniculatus from foraging in the soil layer for insect larvae and seeds.

It would thus seem that more mice would be present on grid 2 but this was

not the case. Tevis (1956b) noted that higher numbers of Peromyscus

maniculatus were found on slash areas and he suggested that the advantage

to mice of such areas is related to the density of cover and quantity and

variety of food. In cutover areas Tevis (1956b) found that insects constituted

60% of the stomach contents as opposed to 44% of such contents in forested areas.

He concluded that the many   insects   that thrive   in   association

with the vegetation of recently logged areas may be responsible, in part,

for increased numbers of mice. No such relationship was found in this

study. Harling (personal communication, 1972) found few differences in the

dietary habits between mice taken from slash or forest areas. In areas which

have been logged and burned the colonization by annual plants occurs quickly.

Fireweed (Epilobium augustifolium), bracken (Pteridium aquilinum) and

various grasses invade the area and create a dense vegetational mat

(Kellman, 1969).   After six years   this   vegetational   stage

was   very   well   developed   on area 3.   This   may   explain   the

presence of both Microtus and Peromyscus populations with their different

dietary demands, Microtus being primarily herbivorous whereas Peromyscus

is omnivorous. Lobue and Darnell (1959) have suggested that competition

between these two species is unlikely, basing   their argument on the

fact that Microtus is diurnal and Peromyscus is nocturnal. Peromyscus apparently

prefers less dense vegetation than Microtus. Other authors (Wirtz and

Pearson, 1960; Grant, 1970, 1971) have demonstrated in both field and

laboratory studies that aggressive interspecific interactions between Microtus and Peromyscus occur. Wirtz and Pearson (1960) reported that M. pennsylvanicus was more aggressive than P. leucopus and Grant (1971) stated that M. pennsylvanicus excluded P. maniculatus from grassland habitats when the former species was high in number. In this study it was difficult to determine which factors were affecting the reciprical nature of the changes in numbers of M. oregoni and P. m. austerus populations on grid 3. It should be noted that M. oregoni frequently occupies forest habitats (Ingles, 1965) although the frequency of its capture on grid 1 and 2 was extremely low (Table 13). Therefore it would seem that the changes in populations of the two species could possibly be the result of some type of competitive interaction. The reason as to the declines of both the Microtus and Peromyscus population in the late summer of 1970 cannot be explained. Lobue and Darnell (1959) have also suggested that habitats such as grid 3 are not conducive to Peromyscus.

LOGGING EFFECTS

Logging does not adversely effect the mouse populations, in fact areas which have just been logged seem to be very attractive. Area 2 populations (Fig. 5) increased considerably after logging. Although logging causes drastic macro-environmental changes there do not seem to be significant changes in the micro-environment which Peromyscus inhabits. Therefore the factor which seems to have the most effect on the population numbers is the various vegetational stages that follow logging, especially the successional stages four years (Plate 4) after logging.

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SLASH BURNING

After logging has been completed there is a large amount of slash which is left behind. Slash consists of interlocking tangles of branches, tops of conifers, splintered trunks, shattered sections of bark, great piles of culled logs and other non-marketable trees. During the summer this slash becomes dry and flammable, thus constituting a fire hazard which is potentially more dangerous than a virgin timber stand. Moreover by covering the ground slash makes the planting of seedlings difficult and also prevents seed from reaching the soil. For these reasons slash burning has become the standard operational procedure, following logging, in British Columbia.

Various authors have suggested that slash burning may be detrimental to small mammal populations (Krauch, 1936; Shirley 1937; Fowells and Schubert, 1951) either by destroying the animals on the area or by driving them out. In 1969, half of area 2 was burned in August to determine the effect such burning had on resident deermice. This area was trapped immediately before burning commenced and soon after burning had ceased. Although the ashes were still warm and various stumps were still burning, mice were caught on this area that evening. During the burn there was no indication of a mass exodus of mice from the area, although mice may have left the area when the fire started and re-invaded during the night from the surrounding area. Tevis (1956b) in a similar experiment found that 33 percent of the mice were recaptured on the grid compared with 77 percent

in this study, however the fire described by Tevis (1956b) seems to have been more intense, this being based on the amount of ash left after burning. In the months after burning there was no indication in the trapping records that the deermouse avoided the burnt areas as captures on it were just as frequent as those on the unburned area (Table 14) $x^2 = 2.24$ N.S.).

CONTROL

There have been attempts at protecting Douglas fir seeds used in aerial reseeding by either poisoning the area prior to their distribution or by impregnating the seeds with either sodium fluoroacetate (1080), thallous sulphate (Radwan, 1963) or endrin (Radwan, Crouch and Ellis, 1970). These preventive methods have not been very successful (Radwan, 1963). Poisoning techniques have failed because in the Douglas fir region the two most commonly used poisons 1080 and thallous sulphate are applied directly to Douglas fir seeds. Consequently, the poison is concentrated in the hulls which the rodents usually cut through but do not eat and the animal does not consume much of the poison (Radwan, 1963). The use of endrin although effective, can not be continued because of its high toxicity to all heterotrophic organisms (Radwan et al., 1970) Crouch and Radwan (1971) have reported that by using an antifertility chemical, mestranol, at a two percent concentration consumption of seeds was reduced and germination rates were not affected.

Table 14. Total number of captures on burned and

unburned area of grid 2.

	BURNED AREA	UNBURNED AREA
Before Burn	187 (32%)	395 (78%)
After Burn	131 (37%)	224 (73%)
Number Trap Stations	40	80

$\chi^2 = 2.24$ n.s. at $P \leq 0.05$.

Aerial reseeding has usually been conducted in the fall. At this time most rodent populations are at their peak so that the success of such an operation is doubtful. Hooven (1958) has reported that two mice per 0.5 hectare can consume up to 300 Douglas fir seeds per night. Half a pound of seed is normally distributed over such an area and this amount could be easily consumed by deermice at this low density in 35 nights. Spencer (1954) has noted that the presence of deermice has been shown to almost nullify attempts to aerially reseed in various parts of Washington and Oregon. Casperson (personal communication, 1972) has estimated that the bare minimum requirement for feral deermice would be approximately 150 seeds per night. Such reseeding programs would thus be severely curtailed by the presence of deermice. Suggestions as to the control of deermice populations are very difficult to make since it is the most ubiqutous of all forest rodents. The problem is also complicated by the deermice's high mobility and exploratory nature. Even if areas could be cleared of deermice by either trapping or poisoning, reinvasion will occur almost immediately (Sadleir, 1965, Healey, 1967, Fordham, 1971). A promising method is being developed by J. Walters, the Director of the U.B.C. Research Forest. This method involves aerially restocking an area by dropping small seedlings which have their roots in a soil pack encased in a 10 to 12 centimetre long biodegradable plastic bullet. These seedlings upon hitting the ground become embedded in the soil and as the seedlings begin to grow the plastic case is ruptured. Deermice do not attack seedlings as readily as they do seeds Although voles may do so.

A possible solution to successfully restocking logged forest areas by aerial reseeding lies in distributing Douglas fir seed in a form which is unpalatable to deermice. Attempts at trapping or poisoning populations have failed as they must result in 100% mortality as well as curtailing immigration. Possible solutions to this problem would be in the development of non-toxic repellents which would discourage consumption. Mestranol (Crouch and Radwan, 1971) seems to have this effect but its high cost prevents its use in a large scale situation. Other possible means of restocking would be to aerially distribute recently germinated Douglas fir seed or to bring Douglas fir seeds to within a few hours or days of germination in an optimum environment, as deermice will not attack germinated seeds (Radwan, et al., 1970) and then broadcast them aerially. This would reduce the period of risk to predation. In summary it would seem that use of non-toxic repellents on seeds, as well as distributing seeds in periods when the Peromyscus population is low would be a more efficient and practical method of reforesting large areas and is certainly worthy of further investigation.

SUMMARY AND CONCLUSIONS

1. Home ranges of deermice were estimated by trapping and smoked paper methods. Using the combined ranges as 100%, traps revealed an average of 44% of the range and smoked paper 82%. The smoked paper system showed the lower variability in estimating the range.

2. Males covered considerably larger areas in the breeding season than do either males or females at any other time. This increased movement was attributed to behavioural and physiological factors.

3. In both sexes the size of home ranges continued to increase as more captures were made. This inherent limitation, which has not been previously reported, prevented valid comparisons of mean home range areas in different habitats.

4. Peromyscus maniculatus does not appear to have a well defined home area. A central area is apparently used intensively but there are occasional sallies outwards for a greater distance so that the home range resembles the hub and spokes of a wheel.

5. Population changes during breeding seasons are a direct function of the number of the young produced and their survival. The population on grid 3 disappeared in August 1970.

6. The probability of survival, in the breeding season, had considerably less effect on population numbers than recruitment, even during periods of low survival.

7. In most breeding seasons, recruitment more than compensates for the effects of mortality. This appears to be a more important parameter in the breeding season than survival.

8. The viability of a population from one year to the next appears to depend mainly on the number of mice present at the end of breeding.

9. Factors such as weather, parasitism, predation and disease did not seem to affect population levels.

10. From the analysis of the population data, it was possible to deduce a generalized scheme of events which was consistent with the fluctuations of all three populations of deermice. The most important factors affecting the changes in numbers are recruitment and length of the non-breeding season.

11. Aggressive behaviour was studied in paired bouts in 1970 and is related to testes development.

12. The highest number of aggressive acts occurred in May 1970. The seasonal changes in aggression seen followed those reported by previous workers.

13. A relationship was noted between the level of aggressiveness and the home ran area occupied but the advantage of this relationship is not known.

14. Logging practice and slash burning did not affect the mouse populations adversely. The vegetational stages after logging seem to determine the population levels.

15. Present methods of chemical or physical control of Peromyscus as a seed predator have been largely unsuccessful.

16. Suggestions as to optimum seeding time or methods of by-passing the seed stage of reforestation are discussed.

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APPENDIX 1

The use of index trap lines to estimate population numbers of deermice (*Peromyscus maniculatus*) in a forest environment in British Columbia

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Monthly live trapping of three 1-hectare grids in differing forest habitats was carried out over an 8-month period. Immediately after 2 nights of trapping on each grid a central index line was trapped for a further 2 nights. The total capture numbers, numbers of males, and numbers of females of deermice (*Peromyscus maniculatus*) on the index line correlated significantly with the same parameters on the grid. In addition, survival rates and body weights were almost identical and similar representation of other small mammal species was determined by both arrangements of traps. It is suggested that the index line may be a more efficient method of sampling small mammal populations.

Introduction

General statements regarding seasonal changes in population numbers of small mammals in different types of habitat require sampling of large areas. Trapping exceedingly large grids is time consuming, but comparable data can often be obtained from either a number of small grids or combinations of grids and index lines. However, the use of lines must be related experimentally to the use of grids as indicators of numbers of animals on a specified area. Such an approach has been described by Brant (1962) using a live trapping and release technique. He found a close relationship between density estimates of three species of small mammal on a single 28-acre grid and density estimates based on two trap lines running through the grid. Hansson (1967) described a relationship between the densities of four small mammal species on index lines and on a small grid in a Swedish forest. Linn (1968) has discussed the theory of index trapping of small mammals. In this paper we report an attempt to relate population numbers as determined by live trapped index lines to densities on live trapped grids in various forest environments.

Methods

Three 1-hectare grids (100 m × 100 m) with 121 stations spaced 10 m apart were trapped at 4-week or longer intervals. One Longworth live trap was set inside a 2-meter radius of each station. Traps were baited with whole oats, and Terylene batting was supplied as bedding. The nest boxes of the traps were covered with expanded polystyrene as described by Shaw and Milner (1967). Traps were set on day 1, and checked on the mornings of

days 2 and 3. On day 3 the grid traps were taken up and the index line set. This consisted of 11 stations 10 m apart (the same stations which formed the central line of the grid) at which four Longworth traps were set inside a 2-m radius of each station. The index line traps were checked on days 4 and 5 and the traps taken up on day 5.

Grid 1 was set in 98-year-old Douglas fir (*Pseudotsuga menziesii*), hemlock (*Tsuga heterophylla*), and red cedar (*Thuja plicata*) forest. The ground cover consisted mainly of salal (*Gaultheria shallon*), vine maple (*Acer circinatum*), salmonberry (*Rubus spectabilis*), and assorted ferns (*Polystichum, Struthiopteris*). Grid 2 was set on an area of originally similar forest which was logged in August, 1968. During the study period the main cover was dead unburned slash through which bracken (*Pteridium aquilinum*) and sword fern (*Polystichum munitum*) were emerging. A feature of this area was the considerable proportion of open bare soil caused by the removal of trees during logging. Grid 3 was set on an area which was partially blown down in 1962, logged in 1964, and burned and planted with 2-year-old Douglas fir seedlings in 1965. During the study period this grid was characterized by a summer flush of growth of annuals such as fireweed (*Epilobium angustifolium*) and bracken. There was considerable growth of various grasses (*Luzula* spp.) and alder (*Alnus rubra*), elder (*Sambucus racemosa*), and vine maple with willow (*Salix*) lining a small stream passing through the grid. All grids were located in the University of British Columbia Research Forest at Haney, B.C., and the main species investigated, the deermouse (*Peromyscus maniculatus*), was handled in the field by methods previously described (Sadleir 1965).

Results

The total numbers (and numbers by sex) captured on the grids were compared with those captured on the index lines. Table I presents the results of statistical analysis of the data while Fig. 1 shows the regression lines relating captures on the grids and index lines. The curved lines on Fig. 1 delineate the 5% confidence

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interval within which an average of many observed values of Y, each with the same value of X, could be expected to fall (second method, Campbell 1967). The 5% confidence limits inside which a single value of Y could be expected to fall were about $\pm$ 13 of the mean values for the total numbers, $\pm$ 7 for males, and $\pm$ 7 for females.

Survival rates and mean body weights of line sampled animals were compared with those of the grid samples (Table II). The crude minimum survival rate (p) was calculated as the proportion of animals known to be alive at time $x + 1$ which were released at time x. These rates were not standardized to a fixed time interval as the comparisons necessary were always over the same time period even though these were of differing lengths. Statistical comparison of these proportions is only possible by the use of the chi-squared test but in most cases "expected" values were found to be less than five, thus rendering the test invalid (Campbell 1967). Chi-squares computed were not significant nor was the chi-square value $(= 0.203)$ significant when the summed recaptures and non-recaptures were compared for all the index and grid samples. Comparisons of mean body weights (Table II) were made by the use of "Students" t-test.

TABLE I

Correlation, regression, and analysis of variance comparing captures on grid and index

Value	D.F.	Total numbers	Males	Females
Correlation coefficient, R	16	0.810***	0.823***	0.658**
Regression, A $\pm$ S.E.		5.67 $\pm$ 3.40	3.66 $\pm$ 1.87	4.27 $\pm$ 1.72
B $\pm$ S.E.		1.30 $\pm$ 0.24	1.25 $\pm$ 0.22	0.94 $\pm$ 0.28
Analysis of variance				
Regression M.S. (a)	1	793.035	364.028	117.764
Curvature M.S. (b)	1	3.935	0.011	0.085
Remainder M.S. (c)	15	27.535	11.583	10.295
$F_1 = b/c$		0.014	0.001	0.008
$F_2 = a/c$		28.800**	31.428**	11.439**

**1% significant, ***0.1% significant.
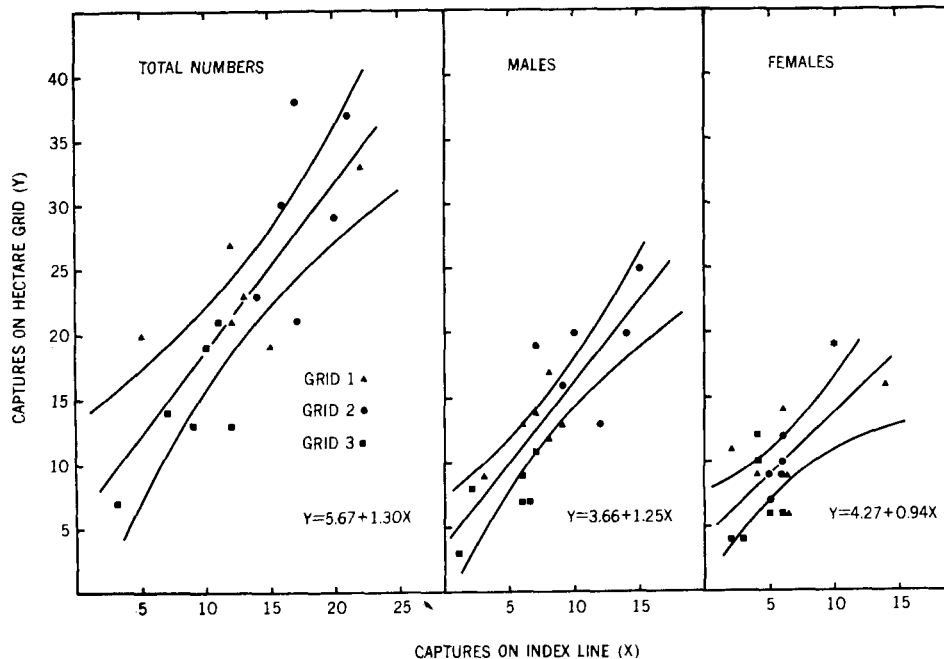
FIG. 1. Scatter diagrams, regression lines, and confidence intervals comparing captures on index lines and hectare grids.

TABLE II

Comparison of survival rates and body weights (by sex) as determined from grid and index trapping

Grid	Monday of week of trapping and release	Weeks at large	Survival rates, p				Body weights										
			Grid		Index		Males					Females				
			Number released	p	Number released	p	Grid		Index		t	Grid		Index		t
							x̄	S.D.	x̄	S.D.		x̄	S.D.	x̄	S.D.	
1	2 Dec. 68	12	33	0.24	21	0.04	15.82	2.84	15.60	3.32	0.17	15.25	4.06	13.50	4.77	1.10
1	25 Feb. 69	8	19	0.53	5	0.60	16.00	1.77	15.66	1.22	0.30	14.60	1.90	16.50	2.12	1.48
1	21 Apr. 69	4	21	0.58	12	0.58	16.66	3.16	17.62	2.57	0.72	17.11	4.96	18.00	0.81	0.34
1	19 May 69	4	19	0.55	15	0.60	16.23	2.78	15.44	3.14	0.64	18.50	1.87	17.16	3.21	0.89
1	16 June 69	4	23	0.65	13	0.54	15.14	2.75	16.00	2.52	0.69	16.62	2.35	15.50	3.02	0.85
1	14 July 69	—	—	—	—	—	16.08	2.50	15.83	2.93	0.73	15.50	3.00	15.50	3.74	0.00
2	19 Nov. 68	16	38	0.38	15	0.33	14.52	4.23	14.14	3.94	0.21	15.26	4.67	14.00	4.24	0.72
2	10 Mar. 69	4	22	0.91	13	0.92	18.73	1.06	19.00	1.20	0.53	18.43	1.57	17.80	1.48	0.70
2	7 Apr. 69	4	28	0.64	16	0.69	20.76	1.89	20.66	2.22	0.10	21.22	1.00	21.20	1.30	0.03
2	6 May 69	4	28	0.57	20	0.45	15.40	5.07	15.71	6.26	0.16	17.11	4.26	17.33	4.28	0.10
2	2 June 69	6	35	0.40	20	0.35	14.88	3.84	15.20	4.33	0.25	17.50	4.25	17.66	6.03	0.06
2	14 July 69	—	—	—	—	—	14.50	3.74	15.00	4.89	0.51	14.90	3.60	17.83	3.60	1.92
3	19 Nov. 68	14	19	0.25	9	0.33	14.85	1.39	14.83	1.62	0.02	15.25	2.70	14.20	3.12	0.66
3	25 Feb. 69	8	6	0.66	3	0.66	16.33	—	20.00	—	—*	13.75	—	14.50	—	—*
3	21 Apr. 69	4	13	0.54	8	0.38	16.60	3.28	17.33	2.96	0.44	18.75	2.75	18.00	2.17	0.01
3	19 May 69	4	13	0.80	12	0.75	16.71	1.73	17.50	1.76	0.83	17.33	3.07	17.50	3.70	0.20
3	16 June 69	4	20	0.45	10	0.50	16.80	2.86	18.00	3.00	0.83	17.90	4.02	17.50	2.06	0.64
3	14 July 69	—	—	—	—	—	17.38	2.50	18.00	2.83	0.58	18.67		19.60		

*$N_{grid} + N_{index} < 10$.

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TABLE III

Numbers of captures

	Grid	Index
Peromyscus maniculatus	414	233
Microtus oregoni	111	50
Sorex vagrans	64	6
Eutamius amoenus	27	19
Tamiasciurus douglasi	1	3
Glaucomys sabrinus	1	4
Neurotrichus gibbsi	2	1
Clethrionomys gapperi	1	0
Trap "nights"*	2178	792

*See text.

A number of other species of small mammal were captured during this study and their distribution on the two types of trapping is shown in Table III. In this table a trap "night" refers actually to one trap set for 2 nights since an animal captured on 2 adjacent nights is only considered a single capture. Of the four most abundant species only the shrew, *Sorex vagrans*, has a strongly biased capture, as it dies in the grid traps, and thus cannot be trapped later. Except for shrews, the index method gave much the same species representation as the grid.

Discussion

If samples of animals captured by a line trapping method are to be related to samples captured on a grid of traps, it must first be demonstrated that both trap placements are sampling the same trappable population. This can be assumed if the population parameters determined from index line samples are in close agreement with those found on the grid as a whole. Characteristics such as numbers captured, sex ratios, weights, survival, and species composition can be easily compared but the parameter of density cannot be calculated by an index line because the sample is linear with unknown spatial properties.

The numbers of deermice captured over 2 nights on the index line correlated well with the numbers captured during 2 nights on the grid. Thus the index line could be used to determine fluctuations in the abundance of deermice in these forest environments. Moreover, the regression line allows estimation of the average density of animals on a hypothetical hectare grid from a sample taken on an isolated index line although the variation of such an estimate is large (Fig. 1). Stickel (1948) considered that single lines of traps could not be used as a reliable means of measuring the relative abundance of animals because she found that the numbers of animals caught in two types of habitat differed between grid and index. Figure 1 includes data from three different habitats, none of which shows any consistent differences in proportion.

Significant correlations and regressions were noted when sexes were treated separately. The differences between males and females is understandable as many studies of small mammals (excellently reviewed by Brown 1962, 1966) have shown home ranges of males are larger than those of females and this is also true for *P. maniculatus* (Allred and Beck 1963). However, the correlations and regressions allow for estimates of the numbers of males and females independently on the hypothetical hectare around a standard index line.

Despite the necessarily low numbers released from the index trapping, the survival rates determined from both samples are very similar even over differing periods of time (Table II). No explanation can be offered for the apparently different survivals on grid 1 from December to February. Considerable seasonal changes in mean body weights were seen on all areas and the weights differed between grids and sexes, but both the grid and index samples show similar mean weights. The *t*-test indicated no significant differences.

It would thus appear that the 100-m index trapping system can give an excellent indication of the population parameters over 1 hectare. This being so, index lines could be used to sample deermice populations over a considerably greater area for the same expenditure of time and energy that is involved in setting up and maintaining a single grid. It would obviously be necessary to test, occasionally, the representativeness of the index line by temporarily setting up a grid around it, especially if this technique of sampling is attempted for other species of small mammals, or in environments other than the coastal forest of British Columbia. However, the success of this investigation would suggest that the use of index lines as indices of population changes is a technique worthy of reinvestigation by workers studying small mammals.

Acknowledgments

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APPENDIX 2

Mean N and Variance

$$\bar{N} = \sum_{i=n_1}^{n_2} a_i N_i$$

$$\text{Var } \bar{N} = \sum_{i=n_1}^{n_2} a_i^2 \text{ Var } N_i + 2 \sum_{i=n_1}^{n_2-1} \sum_{t=i+1}^{n_2} a_i a_t \text{ Cov}\left(N_i, N_t\right)$$

a_i is a weighting factor given to the i th sample period in computing $\bar{N}$ where the sampling periods of the two N runs do not coincide. Its calculation is shown in the following theoretical example. Assume comparison of $\bar{N}$'s is required from week 62 to week 70 from area A sampled on weeks, 58, 63, 64, 68 and 75 and from area B sampled as week 58, 62, 66, 70 and 75. Estimates of N must be made for those weeks in which N determinations were not coincident.

$$\bar{N}^A_{62-70} = 1/6 \left[\left(4/5\ N^A_{63} + 1/5\ N^A_{58}\right) + N^A_{63} + N^A_{64} + \left(2/4\ N^A_{68} + 2/4\ N^A_{64}\right) + N_{68} \right.$$
$$\left. + \left(2/7\ N^A_{75} + 5/7\ N^A_{68}\right) \right]$$

$$= 1/6 \left[1/5\ N^A_{58} + 9/5\ N^A_{63} + 6/4\ N^A_{64} + 62/28\ N^A_{68} + 2/7\ N^A_{75} \right]$$

$$= 1/30\ N^A_{58} + 3/10\ N^A_{63} + 1/4\ N^A_{64} + 31/84\ N^A_{68} + 1/21\ N^A_{75}$$

The fraction before each N value is its separate a_i (N.B. $\Sigma a_i = 1$) Similar calculations are then carried out for the B area with other N estimates inserted and $\bar{N}$ calculated.

APPENDIX 3

TABLE OF CUMULATIVE TOTALS (THE A(I,J))

PEROMYSCUS   AREA 1   CONTROL   HANEY

MALES

(Table of cumulative totals, rows and columns indexed by values 60, 64, 68, 73, 79, 87, 91, 95, 99, 103, 107, 111, 115, 119, 123, 127, 131, 136, 140, 144, 148, 152, 156, 160, 164, 168, 172, 176, 180; body consists predominantly of zeros with scattered nonzero counts.)

THE SUMS A(I,J)

THE SUMS N(I,J)

PEROMYSCUS AREA 1 CONTROL HANEY

MALES

WEEK OF CAPTURE

WEEK OF LAST CAPTURE

WEEK OF LAST CAPTURE	60	64	68	73	79	87	91	95	99	103	107	111	115	119	123	127	131	136	140	144	148	152	156	160	164	168	172	176	180
60	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
64	0	5	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
68	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
73	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
79	0	0	0	0	3	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
87	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
91	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
95	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
99	0	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
103	0	0	0	0	0	0	0	0	7	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
107	0	0	0	0	0	0	0	0	0	1	0	7	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
111	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
115	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
119	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
123	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
127	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
131	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	3	3	0	0	0	0	0	0	0	0	0	0	0
136	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	3	3	0	0	0	0	0	0	0	0	0	0
140	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	3	3	0	3	1	0	0	0	0	0
144	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
148	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
152	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
156	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	3	0	0	0	0
160	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
164	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
168	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0
172	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0
176	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2

TOTAL MARKED

| 0 | 3 | 5 | 6 | 8 | 3 | 3 | 4 | 8 | 5 | 6 | 6 | 9 | 8 | 10 | 11 | 9 | 4 | 5 | 3 | 4 | 6 | 3 | 5 | 2 |

TOTAL UNMARKED

| 6 | 3 | 7 | 5 | 10 | 1 | 6 | 8 | 6 | 9 | 1 | 2 | 2 | 1 | 9 | 7 | 5 | 1 | 1 | 2 | 4 | 7 | 4 | 8 |

TOTAL CATCH

| 6 | 6 | 12 | 11 | 18 | 4 | 9 | 9 | 14 | 15 | 17 | 13 | 10 | 13 | 11 | 9 | 5 | 7 | 8 | 8 | 8 | 10 | 10 | 9 | 10 |

TOTAL RELEASED

| 5 | 6 | 12 | 10 | 18 | 3 | 8 | 9 | 14 | 15 | 17 | 13 | 10 | 13 | 11 | 9 | 5 | 7 | 8 | 8 | 8 | 10 | 10 | 9 | 10 |

POPULATION PARAMETERS ESTIMATED FROM MULTIPLE RECAPTURE DATA - JOLLYS STOCHASTIC MODEL

PEROMYSCUS AREA 1 CONTROL HANEY

MALES

WEEK	ALPHA	M	N + 4 SE	PHI + 4 SE	B+ 4 SE	LAMBDA + 4 SE
				WEEK OF CAPTURE		
WEEK OF LAST CAPTURE						
60	0.0	0.0	0.0 + 0.0	0.600 + 0.876	0.0 + 0.0	0.0 + 0.0
64	0.5000	3.00	6.0 + 4.9	0.833 + 0.609	7.0 + 0.0	2.400 + 0.167
68	0.4167	5.00	12.0 + 5.5	0.604 + 0.598	6.0 + 6.4	1.833 + 0.091
73	0.5455	7.25	13.3 + 10.6	0.940 + 0.839	12.2 + 17.0	2.059 + 0.179
79	0.4444	10.57	23.8 + 24.4	0.875 + 2.650	3.2 + 30.4	1.153 + 0.129
87	0.7500	18.00	24.0 + 76.5	0.611 + 2.202	18.9 + 65.9	2.348 + 1.428
91	0.3333	11.00	33.0 + 82.3	0.411 + 0.763	1.6 + 29.4	1.125 + 0.377
95	0.4444	6.57	14.8 + 20.3	0.826 + 0.625	4.5 + 13.8	1.370 + 0.141
99	0.5714	9.56	16.7 + 14.8	0.716 + 0.653	6.6 + 9.5	1.550 + 0.066
103	0.6000	11.14	18.6 + 17.2	0.467 + 0.515	8.3 + 4.4	1.962 + 0.141
107	0.4706	8.00	17.0 + 10.0	0.625 + 0.533	4.7 + 4.8	1.444 + 0.022
111	0.6923	10.63	15.3 + 12.7	0.615 + 0.540	3.4 + 6.0	1.361 + 0.041
115	0.7000	9.00	12.9 + 11.1	1.007 + 0.039	1.3 + 5.4	1.103 + 0.013
119	0.8462	12.08	14.3 + 10.2	0.970 + 0.357	1.2 + 3.6	1.085 + 0.005
123	0.9091	13.67	15.0 + 11.3	0.989 + 0.776	2.9 + 7.2	1.192 + 0.015
127	0.8182	14.50	17.7 + 17.4	0.594 + 0.691	0.5 + 5.0	1.047 + 0.015
131	0.8889	9.80	11.0 + 12.0	0.679 + 0.970	1.7 + 6.1	1.224 + 0.044
136	0.8000	7.33	9.2 + 14.5	0.600 + 0.876	1.5 + 3.9	1.273 + 0.060
140	0.7143	5.00	7.0 + 8.1	0.619 + 0.856	1.4 + 3.8	1.333 + 0.065
144	0.7500	4.33	5.8 + 9.1	0.750 + 0.866	0.7 + 3.1	1.154 + 0.046
148	0.8000	4.00	5.0 + 6.8	0.600 + 0.876	2.0 + 0.0	1.667 + 0.111
152	0.6000	3.00	5.0 + 6.0	1.000 + 1.265	8.3 + 18.7	2.667 + 0.842
156	0.3750	5.00	13.3 + 23.6	0.560 + 0.839	3.7 + 13.9	1.500 + 0.386
160	0.5000	5.60	11.2 + 14.5	0.625 + 0.685	1.0 + 6.3	1.143 + 0.068
164	0.7500	6.00	8.0 + 8.2	0.375 + 0.685	7.0 + 0.0	3.333 + 1.490
168	0.3000	3.00	10.0 + 6.3	0.600 + 0.620	4.0 + 0.0	1.667 + 0.041
172	0.6000	6.00	10.0 + 7.3	0.500 + 0.632	4.0 + 0.0	1.800 + 0.085
176	0.5556	5.00	9.0 + 10.8	0.0 + 0.0	0.0 + 0.0	5.000 + 0.0
180	0.2000	0.0	0.0 + 0.0	0.0 + 0.0	0.0 + 0.0	0.0 + 0.0

ALPHA IS PROPORTION OF MARKED ANIMALS
M IS TOTAL MARKED POPULATION
N IS TOTAL POPULATION
PHI IS PROBABILITY OF SURVIVAL
B IS NUMBER OF NEW ANIMALS JOINING THE POPULATION
LAMBDA IS DILUTION RATE (AS DEFINED BY JOLLY)

STANDARDIZED 28-DAY RATES + 4 SE LIMITS

PEROMYSCUS AREA 1 CONTROL HANEY

MALES

WEEK	INST. DEATH RATE	SURVIVAL RATE	DILUTION RATE
60	-0.511 (-1.971 TO 0.950)	0.600(-.276 TO 1.476)	0.0 (0.0 TO 0.0)
64	-0.182 (-0.913 TO 0.548)	0.833(0.225 TO 1.442)	2.400 (0.866 TO 3.934)
68	-0.403 (-1.155 TO 0.389)	0.668(0.139 TO 1.198)	1.624 (0.770 TO 2.478)
73	-0.041 (-0.637 TO 0.554)	0.959(0.388 TO 1.530)	1.619 (0.731 TO 2.506)
79	-0.067 (-1.581 TO 1.448)	0.935(-.481 TO 2.352)	1.074 (0.404 TO 1.744)
87	-0.492 (-4.095 TO 3.110)	0.611(***** TO 2.813)	2.348 (-2.432 TO 7.127)
91	-0.890 (-2.748 TO 0.968)	0.411(-.352 TO 1.174)	1.125 (-1.331 TO 3.581)
95	-0.191 (-0.948 TO 0.565)	0.826(0.201 TO 1.451)	1.370 (-0.133 TO 2.872)
99	-0.334 (-1.245 TO 0.578)	0.716(0.063 TO 1.370)	1.550 (0.525 TO 2.576)
103	-0.762 (-1.866 TO 0.342)	0.467(-.049 TO 0.982)	1.962 (0.461 TO 3.462)
107	-0.470 (-1.322 TO 0.382)	0.625(0.092 TO 1.158)	1.444 (0.849 TO 2.040)
111	-0.486 (-1.363 TO 0.392)	0.615(0.076 TO 1.155)	1.361 (0.548 TO 2.175)
115	0.007 (-0.032 TO 0.046)	1.007(0.968 TO 1.046)	1.103 (0.639 TO 1.567)
119	-0.030 (-0.398 TO 0.338)	0.970(0.613 TO 1.328)	1.085 (0.813 TO 1.357)
123	-0.011 (-0.797 TO 0.774)	0.989(0.212 TO 1.765)	1.192 (0.695 TO 1.690)
127	-0.521 (-1.685 TO 0.643)	0.594(-.097 TO 1.285)	1.047 (0.558 TO 1.537)
131	-0.310 (-1.452 TO 0.833)	0.734(-.104 TO 1.572)	1.176 (0.529 TO 1.823)
136	-0.511 (-1.971 TO 0.950)	0.600(-.276 TO 1.476)	1.273 (0.290 TO 2.256)
140	-0.480 (-1.862 TO 0.903)	0.619(-.237 TO 1.475)	1.333 (0.316 TO 2.351)
144	-0.288 (-1.442 TO 0.867)	0.750(-.116 TO 1.616)	1.154 (0.299 TO 2.009)
148	-0.511 (-1.971 TO 0.950)	0.600(-.276 TO 1.476)	1.667 (0.335 TO 2.999)
152	0.0 (-1.265 TO 1.265)	1.000(-.265 TO 2.265)	2.667 (-1.004 TO 6.337)
156	-0.580 (-2.078 TO 0.918)	0.560(-.279 TO 1.399)	1.500 (-0.986 TO 3.986)
160	-0.470 (-1.565 TO 0.625)	0.625(-.060 TO 1.310)	1.143 (0.097 TO 2.189)
164	-0.981 (-2.807 TO 0.845)	0.375(-.310 TO 1.060)	3.333 (-1.550 TO 8.216)
168	-0.511 (-1.544 TO 0.522)	0.600(-.020 TO 1.220)	1.667 (0.861 TO 2.472)
172	-0.693 (-1.958 TO 0.572)	0.500(-.132 TO 1.132)	1.800 (0.634 TO 2.966)
176	0.0 (0.0 TO 0.0)	0.0 (0.0 TO 0.0)	5.000 (5.000 TO 5.000)
180	0.0 (0.0 TO 0.0)	0.0 (0.0 TO 0.0)	0.0 (0.0 TO 0.0)

TABLE OF CUMULATIVE TOTALS (THE A(I,J))

PERCMYSCUS AREA 1 CONTROL HANEY

FEMALES

	60	64	68	73	79	87	91	95	99	103	107	111	115	119	123	127	131	136	140	144	148	152	156	160	164	168	172	176	180
60	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
64	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
68	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
73	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
79	0	0	0	0	0	3	2	6	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
87	0	0	0	0	0	0	5	0	7	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
91	0	0	0	0	0	0	0	6	3	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
95	0	0	0	0	0	0	0	0	0	0	1	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
99	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
103	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
107	0	0	0	0	0	0	0	0	0	0	0	0	0	10	14	0	0	0	0	1	1	0	0	0	0	0	0	0	0
111	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	8	0	0	0	1	1	1	0	0	0	0	0	0	0
115	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
119	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
123	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
127	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
131	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	3	0	0	0	0	0	0	0	0	0	0
136	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0	0	0	0	0	0	0	0
140	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
144	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4	0	0
148	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	3	0	0	2
152	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	2
156	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6

THE SUMS A(I,J)

| 0 | 0 | 0 | 0 | 3 | 1 | 4 | 1 | 4 | 1 | c | 1 | 2 | 8 | 2 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 2 | 0 |

THE SUMS N(I,J)

| 0 | 4 | 5 | 8 | 6 | 3 | 9 | 4 | 6 | 5 | 8 | 7 | 12 | 14 | 9 | 8 | 7 | 5 | 3 | 3 | 2 | 1 | 2 | 3 | 2 | 4 | 5 | 4 |

DISTRIBUTION OF RECAPTURES ACCORDING TO THE INTERVAL SINCE THEY WERE LAST CAPTURED (METHOD B GROUP).

PEROMYSCUS AREA 1 CONTROL HANEY

FEMALES

WEEK OF CAPTURE

WEEK OF LAST CAPTURE

	60	64	68	73	79	87	91	95	99	103	107	111	115	119	123	127	131	136	140	144	148	152	156	160	164	168	172	176	180
60																													
64		3	4																										
68			4																										
73				8																									
79					2	3																							
87					3		1																						
91						6		4					1																
95							5																						
99									5						1														
103														6		3													
107										7		9	13	1			2												
111													1	5								1							
115												12							2						1				
119															8			3							2				
123																							2						
127																													
131																													
136																													
140																													
144																													
148																													
152																													
156																													
160																													
164																													2
168																												3	
172																											4		
176																													

	60	64	68	73	79	87	91	95	99	103	107	111	115	119	123	127	131	136	140	144	148	152	156	160	164	168	172	176
TOTAL MARKED	0	3	4	5	8	3	5	6	2	3	5	6	7	6	8	12	14	3	2	1	2	2	2	3	4	2	3	6
TOTAL UNMARKED	3	7	4	5	13	1	6	2	3	5	7	4	1	2	1	1	3	2	5	4	4	5	4	2	3	5	4	8
TOTAL CATCH	3	10	8	10	21	4	11	8	10	8	11	14	11	14	15	13	10	7	7	7	10	7	4	4	6	9	7	14
TOTAL RELEASED	3	10	8	10	21	4	11	8	10	8	11	14	11	14	14	13	10	7	7	7	10	7	4	4	6	9	7	14

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POPULATION PARAMETERS ESTIMATED FROM MULTIPLE RECAPTURE DATA - JOLLYS STOCHASTIC MODEL

PEROMYSCUS AREA 1 CONTROL HANEY

FEMALES

WEEK	ALPHA	M	N ± 4 SE		PHI ± 4 SE		B ± 4 SE		LAMBDA ± 4 SE	
				WEEK OF CAPTURE						
60	0.0	0.0	0.0 +	0.0	1.000 +	0.0	0.0 +	0.0	0.0 +	0.0
64	0.3000	3.00	10.0 +	0.0	0.400 +	0.620	4.0 +	0.0	2.000 +	0.150
68	0.5000	4.00	8.0 +	6.2	0.625 +	0.685	5.0 +	0.0	2.000 +	0.112
73	0.5000	5.00	10.0 +	6.7	0.800 +	0.506	13.0 +	0.0	2.625 +	0.140
79	0.3810	8.00	21.0 +	7.4	0.333 +	0.516	2.3 +	8.4	1.333 +	0.096
87	0.7500	7.00	9.3 +	14.9	0.778 +	0.908	6.4 +	10.7	1.886 +	0.336
91	0.4545	6.22	13.7 +	12.7	1.145 +	1.240	3.0 +	15.2	1.190 +	0.066
95	0.7500	14.00	18.7 +	25.5	0.542 +	0.789	2.3 +	8.7	1.224 +	0.064
99	0.7000	8.67	12.4 +	12.4	0.651 +	0.715	2.1 +	5.3	1.256 +	0.038
103	0.7500	7.60	10.1 +	11.5	0.625 +	0.685	4.7 +	2.9	1.737 +	0.099
107	0.5455	6.00	11.0 +	8.4	0.795 +	0.657	8.8 +	9.7	2.000 +	0.117
111	0.5000	8.75	17.5 +	15.4	0.600 +	0.567	4.3 +	9.4	1.414 +	0.081
115	0.6364	9.44	14.8 +	12.9	0.818 +	0.465	3.3 +	6.8	1.268 +	0.032
119	0.7143	11.00	15.4 +	10.4	1.011 +	0.055	0.7 +	3.4	1.045 +	0.003
123	0.9333	15.17	16.3 +	10.1	0.898 +	0.432	1.1 +	2.0	1.077 +	0.002
127	0.9231	13.63	14.8 +	11.3	0.645 +	0.582	2.3 +	3.3	1.239 +	0.011
131	0.8000	9.43	11.8 +	11.1	0.770 +	0.701	1.2 +	4.4	1.131 +	0.017
136	0.8571	8.80	10.3 +	11.7	0.850 +	1.043	1.0 +	4.6	1.114 +	0.020
140	0.8571	8.33	9.7 +	13.7	0.464 +	0.836	1.3 +	4.3	1.280 +	0.076
144	0.7500	4.33	5.8 +	9.4	0.938 +	1.468	1.3 +	6.3	1.231 +	0.099
148	0.7500	5.00	6.7 +	12.8	0.833 +	2.575	1.9 +	11.8	1.350 +	0.268
152	0.6667	5.00	7.5 +	24.0	0.333 +	1.089	2.5 +	4.2	2.000 +	1.046
156	0.4000	2.00	5.0 +	5.7	0.400 +	0.876	2.0 +	0.0	2.000 +	0.382
160	0.5000	2.00	4.0 +	4.9	1.000 +	1.732	4.0 +	13.3	2.000 +	0.595
164	0.5000	4.00	8.0 +	18.6	0.500 +	1.000	2.0 +	6.9	1.500 +	0.459
168	0.5000	3.00	6.0 +	6.2	0.667 +	0.770	5.0 +	0.0	2.250 +	0.234
172	0.4444	4.00	5.0 +	6.2	0.722 +	1.065	8.7 +	22.1	2.333 +	0.687
176	0.4286	6.50	15.2 +	30.1	0.0 +	0.0	0.0 +	0.0	1.615 +	0.0
180	0.4286	0.0	2.0 +	0.0	0.0 +	0.0	0.0 +	0.0	0.0 +	0.0

ALPHA IS PROPRTION OF MARKED ANIMALS
M IS TOTAL MARKED POPULATION
N IS TOTAL POPULATION
PHI IS PROBABILITY OF SURVIVAL
B IS NUMBER OF NEW ANIMALS JOINING THE POPULATION
LAMBDA IS DILUTION RATE(AS DEFINED BY JOLLY)

STANDARDIZED 20-DAY RATES + 4 SE LIMITS

PEROMYSCUS AREA 1 CONTROL HANEY

FEMALES

WEEK	INST. DEATH RATE	SURVIVAL RATE	DILUTION RATE
60	0.0 (0.0 TO 0.0)	1.000(1.000 TO 1.000)	0.0 (0.0 TO 0.0)
64	-0.916 (-2.465 TO 0.633)	0.400(-.220 TO 1.020)	2.000 (0.451 TO 3.549)
68	-0.376 (-1.252 TO 0.500)	0.687(0.085 TO 1.288)	1.741 (0.807 TO 2.675)
73	-0.149 (-0.570 TO 0.273)	0.862(0.498 TO 1.225)	1.903 (1.179 TO 2.627)
79	-0.549 (-1.323 TO 0.224)	0.577(0.131 TO 1.024)	1.155 (0.618 TO 1.692)
87	-0.251 (-1.419 TO 0.916)	0.778(-.130 TO 1.686)	1.886 (-0.433 TO 4.205)
91	0.136 (-0.947 TO 1.218)	1.145(-.095 TO 2.386)	1.190 (0.165 TO 2.216)
95	-0.613 (-2.070 TO 0.844)	0.542(-.247 TO 1.331)	1.224 (0.211 TO 2.237)
99	-0.429 (-1.526 TO 0.669)	0.651(-.064 TO 1.367)	1.256 (0.475 TO 2.038)
103	-0.470 (-1.565 TO 0.625)	0.625(-.060 TO 1.310)	1.737 (0.479 TO 2.995)
107	-0.229 (-1.055 TO 0.557)	0.795(0.138 TO 1.453)	2.000 (0.631 TO 3.369)
111	-0.511 (-1.456 TO 0.433)	0.600(0.033 TO 1.166)	1.414 (0.278 TO 2.551)
115	-0.201 (-0.769 TO 0.368)	0.818(0.353 TO 1.283)	1.268 (0.549 TO 1.988)
119	0.011 (-0.043 TO 0.065)	1.011(0.956 TO 1.066)	1.044 (0.815 TO 1.272)
123	-0.107 (-0.589 TO 0.375)	0.898(0.465 TO 1.332)	1.077 (0.916 TO 1.239)
127	-0.439 (-1.341 TO 0.463)	0.645(0.063 TO 1.226)	1.239 (0.812 TO 1.665)
131	-0.209 (-0.937 TO 0.519)	0.811(0.221 TO 1.402)	1.104 (0.696 TO 1.511)
136	-0.162 (-1.389 TO 1.064)	0.850(-.193 TO 1.893)	1.114 (0.550 TO 1.677)
140	-0.767 (-2.569 TO 1.034)	0.464(-.372 TO 1.301)	1.280 (0.178 TO 2.382)
144	-0.065 (-1.631 TO 1.502)	0.938(-.531 TO 2.406)	1.231 (-0.027 TO 2.488)
148	-0.182 (-3.272 TO 2.907)	0.833(**** TO 3.408)	1.350 (-0.722 TO 3.422)
152	-1.099 (-4.365 TO 2.167)	0.333(-.755 TO 1.422)	2.000 (-2.091 TO 6.091)
156	-0.916 (-3.107 TO 1.275)	0.400(-.476 TO 1.276)	2.000 (-0.471 TO 4.471)
160	0.0 (-1.732 TO 1.722)	1.000(-.732 TO 2.732)	2.000 (-1.086 TO 5.086)
164	-0.693 (-2.693 TO 1.307)	0.500(-.500 TO 1.500)	1.500 (-1.210 TO 4.210)
168	-0.405 (-1.560 TO 0.749)	0.667(-.103 TO 1.436)	2.250 (0.317 TO 4.183)
172	-0.325 (-1.800 TO 1.149)	0.722(-.343 TO 1.787)	2.333 (-0.982 TO 5.648)
176	0.0 (0.0 TO 0.0)	0.0 (0.0 TO 0.0)	1.615 (1.615 TO 1.615)
180	0.0 (0.0 TO 0.0)	0.0 (0.0 TO 0.0)	0.0 (0.0 TO 0.0)

TABLE OF CUMULATIVE TOTALS (THE A(I,J))

PERMYSCUS AREA 2 EXPERIMENTAL HANEY

MALES

	54	58	66	71	77	84	89	93	97	101	105	111	115	119	123	127	131	136	140	144	148	152	156	160	164	168	172	176	180
54	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
58	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
66	0	2	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
71	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
77	0	0	0	3	10	1	1	1	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
84	0	0	0	0	0	8	1	1	1	0	0	1	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
89	0	0	0	0	0	0	12	1	1	0	1	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
93	0	0	0	0	0	0	0	13	14	16	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
97	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
101	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
105	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
111	0	0	0	0	0	0	0	0	0	0	0	0	14	2	15	8	1	0	0	0	0	0	0	0	0	0	0	0	0
115	0	0	0	0	0	0	0	0	0	0	0	0	0	15	10	1	1	0	0	0	0	0	0	0	0	0	0	0	0
119	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	1	12	9	5	5	9	5	6	0	0	0	0	0
123	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
127	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
131	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0
136	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
140	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
144	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
148	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
152	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0
156	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0
160	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	2	0	0	0
164	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
168	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
172	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3
176	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

THE SUMS A(I,J)

| 0 | 0 | 0 | 0 | 3 | 2 | 1 | 0 | 0 | 1 | 1 | 2 | 2 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |

THE SUMS N(I,J)

| 0 | 2 | 3 | 3 | 13 | 7 | 11 | 12 | 14 | 17 | 10 | 15 | 14 | 13 | 12 | 7 | 6 | 11 | 9 | 5 | 6 | 5 | 4 | 6 | 2 | 2 | 2 | 13 |

DISTRIBUTION OF RECAPTURES ACCORDING TO THE INTERVAL SINCE THEY WERE LAST CAPTURED (METHOD B GROUP).

PEROMYSCUS   AREA 2   EXPERIMENTAL   HANEY

MALES

WEEK OF CAPTURE

WEEK OF LAST CAPTURE	54	58	66	71	77	84	89	93	97	101	105	111	115	119	123	127	131	136	140	144	148	152	156	160	164	168	172	176	180
54	0	2	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
58	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
66	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
71	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
77	0	0	0	0	10	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
84	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
89	0	0	0	0	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
93	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
97	0	0	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
101	0	0	0	0	0	0	0	0	0	16	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
105	0	0	0	0	0	0	0	0	0	0	9	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
111	0	0	0	0	0	0	0	0	0	0	0	13	1	1	0	0	0	0	11	0	0	0	0	0	0	0	0	0	0
115	0	0	0	0	0	0	0	0	0	0	0	0	13	13	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0
119	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0
123	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	6	0	0	0	0	0	0	0	0	0	0	0
127	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	5	6	5	0	0	0	0	0	0	0
131	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
136	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0
140	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0
144	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
148	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
152	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
156	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
160	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
164	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
168	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
172	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
176	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13

TOTAL MARKED	0	2	2	3	3	10	8	12	13	14	16	15	14	14	12	6	8	9	5	6	9	5	6	2	11	2	1	3	13
TOTAL UNMARKED	4	1	6	1	16	1	5	3	5	19	8	10	5	3	3	1	6	1	2	4	2	8	2	7	5	9	2	3	3
TOTAL CATCH	4	3	8	4	19	11	13	15	18	33	24	20	19	17	18	11	14	13	8	7	11	13	11	3	16	3	2	1	16
TOTAL RELEASED	3	3	8	4	19	11	13	15	18	32	23	20	19	17	18	11	9	12	14	13	13	8	7	11	11	3	16	3	16

POPULATICN PARAMETERS ESTIMATED FROM MULTIPLE RECAPTURE DATA - JOLLYS STOCHASTIC MODEL

PERCMYSCUS AREA 2 EXPERIMENTAL HANEY

MALES

WEEK	ALPHA	M	N + 4 SE	PHI + 4 SE	B+ 4 SE	LAMBDA + 4 SE
WEEK OF LAST CAPTURE				WEEK CF CAPTURE		
54	0.0	0.0	0.0 + 0.0	0.667 + 1.085	0.0 + 0.0	0.0 + 0.0
58	0.6667	2.00	3.0 + 3.4	0.667 + 1.089	6.0 + 0.0	4.000 + 2.241
66	0.2500	2.00	8.0 + 4.0	0.375 + 0.685	1.0 + 0.0	1.333 + 0.025
71	0.7500	3.00	4.0 + 5.7	0.750 + 0.866	16.0 + 0.0	6.333 + 5.953
77	0.1579	3.00	19.0 + 5.5	0.774 + 0.564	1.5 + 3.6	1.100 + 0.004
84	0.9091	14.71	16.2 + 12.6	0.660 + 0.608	6.2 + 7.7	1.578 + 0.053
89	0.6154	10.36	16.8 + 12.7	0.862 + 0.415	2.0 + 7.0	1.140 + 0.019
93	0.8000	13.25	16.6 + 10.7	0.800 + 0.413	4.8 + 2.3	1.358 + 0.008
97	0.7222	13.00	18.0 + 10.3	0.778 + 0.392	19.0 + 0.0	2.357 + 0.067
101	0.4242	14.00	33.0 + 10.7	0.572 + 0.417	9.1 + 6.7	1.590 + 0.014
105	0.6667	18.30	27.4 + 17.8	0.448 + 0.430	10.8 + 8.3	1.913 + 0.095
111	0.5000	11.33	22.7 + 14.7	0.783 + 0.420	4.9 + 8.0	1.277 + 0.019
115	0.7368	16.71	22.7 + 14.3	0.765 + 0.431	2.8 + 5.7	1.162 + 0.009
119	0.8235	16.62	20.2 + 13.6	0.765 + 0.412	2.6 + 3.1	1.167 + 0.004
123	0.8333	15.00	18.0 + 12.1	0.730 + 0.538	1.3 + 2.8	1.100 + 0.003
127	0.9091	13.14	14.5 + 13.7	0.672 + 0.635	1.0 + 2.9	1.101 + 0.007
131	0.8889	9.50	10.7 + 11.6	0.675 + 0.639	7.0 + 6.7	1.965 + 0.160
136	0.5000	7.09	14.2 + 11.7	0.917 + 0.319	1.0 + 6.1	1.077 + 0.016
140	0.8571	12.00	14.0 + 9.6	0.643 + 0.512	4.0 + 0.0	1.444 + 0.014
144	0.6923	9.00	13.0 + 9.5	0.385 + 0.540	8.0 + 0.0	2.600 + 0.400
148	0.3846	5.00	13.0 + 7.9	0.462 + 0.553	2.0 + 0.0	1.333 + 0.013
152	0.7500	6.00	8.0 + 8.1	0.625 + 0.685	2.0 + 0.0	1.400 + 0.022
156	0.7143	5.00	7.0 + 7.4	0.571 + 0.748	7.0 + 0.0	2.750 + 0.544
160	0.3636	4.00	11.0 + 6.7	0.545 + 0.601	5.0 + 0.0	1.833 + 0.069
164	0.5455	6.00	11.0 + 7.6	0.182 + 0.465	5.0 + 0.0	5.500 + 8.882
168	0.1818	2.00	11.0 + 5.3	0.227 + 0.636	5.0 + 20.8	3.000 + 4.894
172	0.3333	2.50	7.5 + 23.5	0.667 + 1.089	11.0 + 13.9	3.200 + 5.412
176	0.1875	3.00	16.0 + 14.7	0.0 + 0.0	0.0 + 0.0	1.231 + 0.0
180	0.6125	0.0	0.0 + 0.0	0.0 + 0.0	0.0 + 0.0	0.0 + 0.0

ALPHA IS PROPRTICN CF MARKEC ANIMALS
M IS TOTAL MARKED POPULATION
N IS TCTAL POPULATICN
PHI IS PROBABILITY CF SURVIVAL
B IS NUMBER OF NEW ANIMALS JOINING THE POPULATICN
LAMBCA IS DILUTICN RATE(AS DEFINED BY JOLLY)

STANDARDIZED 28-DAY RATES + 4 SE LIMITS

PEROMYSCUS AREA 2 EXPERIMENTAL HONEY

MALES

WEEK	INST. DEATH RATE	SURVIVAL RATE	DILUTION RATE
54	-0.405 (-2.038 TO 1.228)	0.667(-.422 TO 1.755)	0.0 (0.0 TO 0.0)
58	-0.203 (-1.019 TO 0.614)	0.816(0.150 TO 1.483)	2.000 (0.503 TO 3.497)
66	-0.785 (-2.245 TO 0.676)	0.456(-.210 TO 1.123)	1.259 (0.782 TO 1.735)
71	-0.192 (-0.962 TO 0.578)	0.825(0.190 TO 1.461)	3.423 (-0.093 TO 6.940)
77	-0.146 (-0.562 TO 0.270)	0.864(0.505 TO 1.223)	1.056 (0.922 TO 1.190)
84	-0.333 (-1.071 TO 0.405)	0.717(0.188 TO 1.246)	1.440 (0.765 TO 2.115)
89	-0.148 (-0.629 TO 0.333)	0.862(0.448 TO 1.277)	1.140 (0.593 TO 1.688)
93	-0.223 (-0.740 TO 0.293)	0.800(0.387 TO 1.213)	1.358 (0.992 TO 1.725)
97	-0.251 (-0.755 TO 0.253)	0.778(0.386 TO 1.170)	2.357 (1.325 TO 3.390)
101	-0.559 (-1.288 TO 0.170)	0.572(0.155 TO 0.989)	1.500 (1.033 TO 1.967)
105	-0.535 (-1.175 TO 0.104)	0.585(0.211 TO 0.960)	1.541 (0.880 TO 2.202)
111	-0.244 (-0.780 TO 0.292)	0.783(0.363 TO 1.203)	1.277 (0.720 TO 1.834)
115	-0.268 (-0.831 TO 0.296)	0.765(0.334 TO 1.196)	1.162 (0.789 TO 1.536)
119	-0.268 (-0.806 TO 0.270)	0.765(0.353 TO 1.176)	1.167 (0.899 TO 1.434)
123	-0.314 (-1.051 TO 0.422)	0.730(0.192 TO 1.268)	1.100 (0.877 TO 1.323)
127	-0.398 (-1.343 TO 0.547)	0.672(0.037 TO 1.306)	1.101 (0.765 TO 1.436)
131	-0.314 (-1.070 TO 0.442)	0.730(0.178 TO 1.283)	1.717 (0.597 TO 2.836)
136	-0.087 (-0.435 TO 0.261)	0.917(0.598 TO 1.236)	1.077 (0.568 TO 1.586)
140	-0.442 (-1.239 TO 0.355)	0.643(0.131 TO 1.155)	1.444 (0.978 TO 1.911)
144	-0.956 (-2.359 TO 0.448)	0.385(-.155 TO 0.924)	2.600 (0.071 TO 5.129)
148	-0.773 (-1.971 TO 0.425)	0.462(-.092 TO 1.015)	1.333 (0.885 TO 1.781)
152	-0.470 (-1.565 TO 0.625)	0.625(-.060 TO 1.310)	1.400 (0.805 TO 1.995)
156	-0.560 (-1.869 TO 0.750)	0.571(-.177 TO 1.320)	2.750 (-0.202 TO 5.702)
160	-0.606 (-1.707 TO 0.495)	0.545(-.055 TO 1.146)	1.833 (0.783 TO 2.884)
164	-1.705 (-4.263 TO 0.854)	0.182(-.283 TO 0.647)	5.500 (-6.421 TO 17.421)
168	-1.482 (-4.279 TO 1.316)	0.227(-.409 TO 0.863)	3.000 (-5.849 TO 11.849)
172	-0.405 (-2.038 TO 1.228)	0.667(-.422 TO 1.755)	3.200 (-6.105 TO 12.505)
176	0.0 (0.0 TO 0.0)	0.0 (0.0 TO 0.0)	1.231 (1.231 TO 1.231)
180	0.0 (0.0 TO 0.0)	0.0 (0.0 TO 0.0)	0.0 (0.0 TO 0.0)

TABLE CF CUMULATIVE TOTALS (THE A(I,J))

PERCMYSCUS AREA 2 EXPERIMENTAL HANEY

FEMALES

Column headers (left to right): 54 58 66 71 77 84 89 93 97 101 105 111 115 119 123 127 131 136 140 144 148 152 156 160 164 168 172 176 180

Row labels (top to bottom): 54 58 66 71 77 84 89 93 97 101 105 111 115 119 123 127 131 136 140 144 148 152 156 160 164 168 172 176

(The matrix body consists almost entirely of 0 values printed in a dot-matrix / punch-card style grid.)

THE SUMS A(I,J)

THE SUMS N(I,J)

DISTRIBUTION OF RECAPTURES ACCORDING TO THE INTERVAL SINCE THEY WERE LAST CAPTURED (METHOD B GROUP).

PEROMYSCUS AREA 2 EXPERIMENTAL HANEY

FEMALES

WEEK OF CAPTURE

WEEK OF LAST CAPTURE

WEEK OF LAST CAPTURE \ WEEK OF CAPTURE	54	58	66	71	77	84	89	93	97	101	105	111	115	119	123	127	131	136	140	144	148	152	156	160	164	168	172	176	180

(Column headers for recapture matrix, rows labelled by week of last capture: 54, 58, 66, 71, 77, 84, 89, 93, 97, 101, 105, 111, 115, 119, 123, 127, 131, 136, 140, 144, 148, 152, 156, 160, 164, 168, 172, 176.)

	54	58	66	71	77	84	89	93	97	101	105	111	115	119	123	127	131	136	140	144	148	152	156	160	164	168	172	176	180
TOTAL MARKED	0	2	2	4	5	2	4	7	8	9	15	10	6	9	6	4	8	6	6	5	5	6	5	3	2	1	4	5	9
TOTAL UNMARKED	4	4	5	4	15	1	2	5	10	6	3	9	13	1	2	5	1	1	2	2	5	5	6	1	2	8	3	8	3
TOTAL CATCH	4	6	7	8	10	8	10	8	10	15	12	10	15	13	7	7	11	6	6	4	5	6	8	5	4	9	7	13	12
TOTAL RELEASED	4	5	7	7	15	8	10	8	10	14	12	10	15	13	7	7	11	6	6	4	5	6	7	5	4	9	7	13	12

POPULATION PARAMETERS ESTIMATED FROM MULTIPLE RECAPTURE DATA - JOLLYS STOCHASTIC MODEL

PEROMYSCUS   AREA 2   EXPERIMENTAL   HANEY

FEMALES

WEEK	ALPHA	M	N + 4 SE		PHI + 4 SE		B + 4 SE		LAMBDA + 4 SE	
WEEK OF LAST CAPTURE			**WEEK OF CAPTURE**							
54	0.0	0.0	0.0 +	0.0	0.500 +	1.000	0.0 +	0.0	0.0 +	0.0
58	0.3333	2.00	6.0 +	4.9	0.400 +	2.876	5.0 +	0.0	3.500 +	2.344
66	0.2657	2.00	7.0 +	4.9	0.905 +	1.246	6.3 +	13.6	2.000 +	0.230
71	0.5000	6.33	12.7 +	20.3	0.429 +	0.748	14.0 +	6.3	3.800 +	2.483
77	0.2105	4.00	19.0 +	7.3	0.789 +	0.752	2.1 +	6.9	1.143 +	0.013
84	0.8750	15.00	17.1 +	18.1	0.708 +	0.832	2.0 +	7.2	1.167 +	0.027
89	0.8000	11.33	14.2 +	14.0	0.600 +	0.620	0.6 +	3.9	1.076 +	0.016
93	0.8750	8.00	9.1 +	9.6	1.000 +	0.0	0.9 +	1.7	1.094 +	0.003
97	0.9000	9.00	10.0 +	5.5	0.500 +	0.632	10.0 +	0.0	3.000 +	0.625
101	0.3333	5.00	15.0 +	7.9	0.643 +	0.512	3.0 +	0.0	1.333 +	0.007
105	0.7500	9.00	12.0 +	8.9	0.500 +	0.775	9.0 +	16.3	2.500 +	0.578
111	0.4000	6.00	15.0 +	22.1	0.500 +	0.632	7.5 +	8.7	2.000 +	0.419
115	0.4000	6.00	15.0 +	8.8	0.507 +	0.590	3.8 +	9.3	1.500 +	0.110
119	0.6667	7.60	11.4 +	14.3	0.833 +	0.609	3.5 +	7.9	1.368 +	0.089
123	0.6154	8.00	13.0 +	9.0	0.569 +	0.604	1.2 +	2.4	1.167 +	0.009
127	0.8571	7.40	8.6 +	9.9	0.714 +	0.682	0.8 +	1.9	1.135 +	0.010
131	0.6571	6.00	7.0 +	8.2	0.429 +	0.748	2.0 +	0.0	1.667 +	0.123
136	0.6000	3.00	5.0 +	6.3	0.800 +	0.716	2.0 +	0.0	1.500 +	0.037
140	0.6667	4.00	6.0 +	6.2	1.000 +	0.0	5.0 +	0.0	1.833 +	0.046
144	0.5455	6.00	11.0 +	6.2	0.591 +	0.690	1.3 +	2.8	1.200 +	0.014
148	0.8333	6.50	7.8 +	9.2	0.667 +	0.770	0.8 +	2.1	1.154 +	0.017
152	0.8333	5.00	6.0 +	7.3	0.500 +	0.816	2.0 +	0.0	1.667 +	0.115
156	0.6000	3.00	5.0 +	6.1	0.400 +	0.876	2.0 +	0.0	2.000 +	0.393
160	0.5000	2.00	4.0 +	5.0	0.250 +	0.866	8.0 +	0.0	9.000 +	54.286
164	0.1111	1.00	9.0 +	3.7	0.556 +	0.663	8.0 +	0.0	2.600 +	0.254
168	0.3846	5.00	13.0 +	6.3	0.308 +	0.512	3.0 +	0.0	1.750 +	0.106
172	0.5714	4.00	7.0 +	6.9	0.714 +	0.683	8.0 +	0.0	2.600 +	0.303
176	0.3846	5.00	13.0 +	13.2	0.0 +	0.0	0.0 +	0.0	1.333 +	0.0
180	0.7500	0.0	0.0 +	0.0	0.0 +	0.0	0.0 +	0.0	0.0 +	0.0

ALPHA IS PROPRTION OF MARKED ANIMALS
M IS TOTAL MARKED POPULATION
N IS TOTAL POPULATION
PHI IS PROBABILITY OF SURVIVAL
B IS NUMBER OF NEW ANIMALS JOINING THE POPULATION
LAMBDA IS DILUTION RATE(AS DEFINED BY JOLLY)

STANDARDIZED 28-DAY RATES + 4 SE LIMITS

PEROMYSCUS AREA 2 EXPERIMENTAL HANEY

FEMALES

WEEK	INST. DEATH RATE	SURVIVAL RATE	DILUTION RATE
54	-0.693 (-2.693 TO 1.307)	0.500(-.500 TO 1.500)	0.0 (0.0 TO 0.0)
58	-0.458 (-1.554 TO 0.637)	0.632(-.060 TO 1.325)	1.871 (0.234 TO 3.507)
66	-0.080 (-1.181 TO 1.021)	0.922(-.094 TO 1.940)	1.741 (0.406 TO 3.077)
71	-0.565 (-1.729 TO 0.599)	0.568(-.093 TO 1.230)	2.435 (-0.257 TO 5.128)
77	-0.135 (-0.679 TO 0.409)	0.874(0.398 TO 1.349)	1.079 (0.834 TO 1.325)
84	-0.276 (-1.216 TO 0.664)	0.759(0.045 TO 1.472)	1.131 (0.624 TO 1.638)
89	-0.511 (-1.544 TO 0.522)	0.600(-.020 TO 1.220)	1.076 (0.577 TO 1.574)
93	0.0 (0.0 TO 0.0)	1.000(1.000 TO 1.000)	1.094 (0.865 TO 1.322)
97	-0.693 (-1.958 TO 0.572)	0.500(-.132 TO 1.132)	3.000 (-0.162 TO 6.162)
101	-0.442 (-1.239 TO 0.355)	0.643(0.131 TO 1.155)	1.333 (1.002 TO 1.665)
105	-0.462 (-1.495 TO 0.571)	0.630(-.021 TO 1.281)	1.842 (0.348 TO 3.336)
111	-0.693 (-1.958 TO 0.572)	0.500(-.132 TO 1.132)	2.000 (-0.589 TO 4.589)
115	-0.680 (-1.845 TO 0.465)	0.507(-.084 TO 1.097)	1.500 (0.171 TO 2.829)
119	-0.182 (-0.913 TO 0.548)	0.833(0.225 TO 1.442)	1.368 (0.173 TO 2.564)
123	-0.563 (-1.625 TO 0.498)	0.569(-.035 TO 1.174)	1.167 (0.796 TO 1.537)
127	-0.336 (-1.293 TO 0.620)	0.714(0.031 TO 1.397)	1.135 (0.741 TO 1.529)
131	-0.678 (-2.074 TO 0.719)	0.508(-.201 TO 1.217)	1.505 (0.492 TO 2.518)
136	-0.223 (-1.118 TO 0.671)	0.800(0.084 TO 1.516)	1.500 (0.726 TO 2.274)
140	0.0 (0.0 TO 0.0)	1.000(1.000 TO 1.000)	1.833 (0.974 TO 2.693)
144	-0.526 (-1.693 TO 0.641)	0.591(-.099 TO 1.281)	1.200 (0.720 TO 1.680)
148	-0.405 (-1.560 TO 0.749)	0.667(-.103 TO 1.436)	1.154 (0.631 TO 1.676)
152	-0.693 (-2.326 TO 0.940)	0.500(-.316 TO 1.316)	1.667 (0.312 TO 3.021)
156	-0.916 (-3.107 TO 1.275)	0.400(-.476 TO 1.276)	2.000 (-0.507 TO 4.507)
160	-1.386 (-4.850 TO 2.078)	0.250(-.616 TO 1.116)	9.000 (****** TO 38.472)
164	-0.588 (-1.780 TO 0.605)	0.556(-.107 TO 1.218)	2.600 (0.583 TO 4.617)
168	-1.179 (-2.843 TO 0.485)	0.308(-.204 TO 0.820)	1.750 (0.450 TO 3.050)
172	-0.336 (-1.293 TO 0.620)	0.714(0.031 TO 1.397)	2.600 (0.397 TO 4.803)
176	0.0 (0.0 TO 0.0)	0.0 (0.0 TO 0.0)	1.333 (1.333 TO 1.333)
180	0.0 (0.0 TO 0.0)	0.0 (0.0 TO 0.0)	0.0 (0.0 TO 0.0)

TABLE OF CUMULATIVE TOTALS (THE A(I,J))

PEROMYSCUS   AREA 3   5 YR SLASH   HANEY

MALES

	51	55	59	63	72	77	91	95	99	103	107	111	115	119	123	127	131	136	140	144	148	152	156	160	164	168
51	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
55	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
59	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
63	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
72	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
77	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
91	0	0	0	0	0	1	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
95	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
99	0	0	0	0	0	0	0	0	0	0	0	0	1	5	0	0	0	0	0	0	0	0	0	0	0	0
103	0	0	0	0	0	0	0	0	6	0	1	7	5	0	0	0	0	0	0	0	0	0	0	0	0	0
107	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
111	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0
115	0	0	0	0	0	0	0	0	0	0	12	6	0	0	0	0	3	0	0	0	0	0	0	0	0	0
119	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	2	0	0	0	0	0	0	0
123	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
127	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
131	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
136	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0
140	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	3	0	0	0	0
144	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	3	0	0	0
148	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0
152	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
156	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0
16C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0
164	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3

THE SUMS A(I,J)
0   0   0   0   0   0   0   0   0   0   1   2   0   1   2   2   1   0   1   2   0   0   0   0   0

THE SUMS N(I,J)
0   2   1   1   2   1   1   5   5   7   8   13 9   5   6   2   1   3   3   2   3   3

DISTRIBUTION OF RECAPTURES ACCORDING TO THE INTERVAL SINCE THEY WERE LAST CAPTURED (METHOD B GROUP).

PEROMYSCUS AREA 3   5 YR SLASH   HANEY

MALES

WEEK OF LAST CAPTURE

WEEK OF CAPTURE

WEEK OF LAST CAPTURE	51	55	59	63	72	77	91	95	99	103	107	111	115	119	123	127	131	136	140	144	148	152	156	160	164	168
51	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
55		0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
59			0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
63				0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
72					0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
77						2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
91							5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
95								5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
99									6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
103										4	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
107											9	4	1	1	0	1	0	0	0	0	0	0	0	0	0	0
111												12	5	5	0	0	0	0	0	0	0	0	0	0	0	0
115													0	0	0	0	0	0	0	0	0	0	0	0	0	0
119														0	0	0	0	0	0	0	0	3	0	0	0	0
123															0	0	2	3	0	0	0	0	0	0	0	0
127																0	0	0	0	0	0	0	0	0	0	0
131																	0	0	0	0	0	0	0	0	0	0
136																		0	0	0	0	0	0	0	0	0
140																			0	0	0	0	0	0	0	0
144																				0	0	0	0	0	0	0
148																					0	0	0	0	0	0
152																						0	0	0	0	0
156																							0	0	0	0
160																								0	3	0
164																									0	3

TOTAL MARKED
0 2 2 1 2 1 1 2 4 5 6 5 1 1 6 7 11 12 6 5 1 3 3 2 3 3

TOTAL UNMARKED
3 1 2 3 1 6 2 4 4 6 10 9 3 1 1 2 1 1 3

TOTAL CATCH
3 3 4 2 8 3 5 9 8 12 15 20 15 7 6 2 3 4 3 4 5 4 6

TOTAL RELEASED
3 3 4 2 8 3 5 9 8 12 15 20 15 7 6 2 3 4 3 4 5 4 6

POPULATION PARAMETERS ESTIMATED FROM MULTIPLE RECAPTURE DATA - JOLLYS STOCHASTIC MODEL

PEROMYSCUS AREA 3 5 YR SLASH HANEY

MALES

WEEK	ALPHA	M	N + 4 SE		PHI + 4 SE		B+ 4 SE		LAMBDA + 4 SE	
WEEK OF LAST CAPTURE					WEEK OF CAPTURE					
51	0.0	0.0	0.0 +	0.0	0.667 +	1.089	0.0 +	0.0	0.0 +	0.0
55	0.6667	2.00	3.0 +	3.3	0.667 +	1.089	2.0 +	0.0	2.000 +	0.241
59	0.5000	2.00	4.0 +	3.9	0.250 +	0.866	3.0 +	0.0	4.000 +	7.292
63	0.2500	1.00	4.0 +	3.6	0.250 +	0.866	1.0 +	0.0	2.000 +	0.801
72	0.5000	1.00	2.0 +	3.6	1.000 +	0.0	6.0 +	0.0	4.000 +	1.801
77	0.2500	2.00	8.0 +	3.6	0.125 +	0.468	2.0 +	0.0	3.000 +	3.550
91	0.3333	1.00	3.0 +	3.8	0.333 +	1.089	4.0 +	0.0	5.000 +	12.244
95	0.2000	1.00	5.0 +	3.5	1.000 +	0.0	4.0 +	0.0	1.800 +	0.020
99	0.5556	5.00	9.0 +	3.5	0.556 +	0.662	3.0 +	0.9	1.600 +	0.035
103	0.6250	5.00	8.0 +	6.3	0.938 +	0.573	7.5 +	8.6	2.000 +	0.113
107	0.5000	7.50	15.0 +	12.5	0.756 +	0.705	0.3 +	7.6	1.029 +	0.029
111	0.8750	10.20	11.7 +	11.7	0.744 +	0.899	16.3 +	26.6	2.882 +	0.717
115	0.3333	8.33	25.0 +	31.6	0.600 +	0.506	5.0 +	16.4	1.333 +	0.137
119	0.5500	11.00	20.0 +	11.1	0.750 +	0.662	3.8 +	5.1	1.250 +	0.007
123	0.8000	15.00	18.8 +	18.1	0.333 +	0.487	0.8 +	2.3	1.120 +	0.013
127	0.6571	6.00	7.0 +	9.0	1.143 +	1.602	1.6 +	4.9	1.200 +	0.021
131	0.8333	8.00	9.6 +	17.7	0.556 +	1.832	4.7 +	28.6	1.875 +	1.585
136	0.5000	5.00	10.0 +	38.4	0.500 +	1.414	-1.0 +	13.9	0.800 +	0.313
140	0.7500	3.00	4.0 +	6.3	0.250 +	0.866	2.0 +	0.0	3.000 +	3.629
144	0.3333	1.00	3.0 +	3.8	0.667 +	1.089	1.0 +	0.0	1.500 +	0.067
148	0.6667	2.00	3.0 +	4.1	1.000 +	0.0	1.0 +	0.0	1.333 +	0.013
152	0.7500	3.00	4.0 +	4.1	0.750 +	0.866	1.0 +	0.0	1.333 +	0.017
156	0.7500	3.00	4.0 +	4.7	0.500 +	1.000	3.0 +	0.0	2.500 +	0.753
160	0.4000	2.00	5.0 +	4.6	0.600 +	0.876	1.0 +	0.0	1.333 +	0.021
164	0.7500	3.00	4.0 +	6.6	0.0 +	0.0	0.0 +	0.0	2.000 +	0.0
168	0.5000	0.0	0.0 +	0.0	0.0 +	0.0	0.0 +	0.0	0.0 +	0.0

ALPHA IS PROPRTION OF MARKED ANIMALS
M IS TOTAL MARKED POPULATION
N IS TOTAL POPULATION

PHI IS PROBABILITY OF SURVIVAL
B IS NUMBER OF NEW ANIMALS JOINING THE POPULATION
LAMBDA IS DILUTION RATE(AS DEFINED BY JOLLY)

STANDARDIZED 28-DAY RATES + 4 SE LIMITS

PEROMYSCUS AREA 3 5 YR SLASH HANEY

MALES

WEEK	INST. DEATH RATE	SURVIVAL RATE	DILUTION RATE
51	-0.405 (-2.038 TO 1.228)	0.667(-.422 TO 1.755)	0.0 (0.0 TO 0.0)
55	-0.405 (-2.038 TO 1.228)	0.667(-.422 TO 1.755)	2.000 (0.037 TO 3.963)
59	-1.386 (-4.850 TO 2.078)	0.250(-.616 TO 1.116)	4.000 (-6.801 TO 14.801)
63	-0.616 (-2.156 TO 0.923)	0.540(-.291 TO 1.371)	1.361 (0.278 TO 2.443)
72	0.0 (0.0 TO 0.0)	1.000(1.000 TO 1.000)	3.031 (-0.224 TO 6.286)
77	-0.594 (-1.663 TO 0.475)	0.552(-.038 TO 1.142)	1.369 (0.386 TO 2.351)
91	-1.099 (-4.365 TO 2.167)	0.333(-.755 TO 1.422)	5.000 (-8.997 TO 18.997)
95	0.0 (0.0 TO 0.0)	1.000(1.000 TO 1.000)	1.800 (1.240 TO 2.360)
99	-0.588 (-1.780 TO 0.605)	0.556(-.107 TO 1.218)	1.600 (0.847 TO 2.353)
103	-0.065 (-0.676 TO 0.546)	0.938(0.365 TO 1.510)	2.000 (0.653 TO 3.347)
107	-0.280 (-1.214 TO 0.653)	0.756(0.050 TO 1.461)	1.029 (0.344 TO 1.713)
111	-0.296 (-1.504 TO 0.913)	0.744(-.155 TO 1.643)	2.882 (-0.505 TO 6.270)
115	-0.511 (-1.354 TO 0.332)	0.600(0.094 TO 1.106)	1.333 (-0.145 TO 2.811)
119	-0.288 (-1.170 TO 0.595)	0.750(0.088 TO 1.412)	1.250 (-0.905 TO 1.595)
123	-1.099 (-2.559 TO 0.362)	0.333(-.154 TO 0.820)	1.120 (0.669 TO 1.571)
127	0.134 (-1.268 TO 1.535)	1.143(-.459 TO 2.745)	1.200 (0.615 TO 1.785)
131	-0.470 (-3.109 TO 2.169)	0.625(**** TO 2.274)	1.653 (-1.899 TO 5.206)
136	-0.693 (-3.522 TO 2.135)	0.500(-.914 TO 1.914)	0.800 (-1.437 TO 3.037)
140	-1.386 (-4.850 TO 2.078)	0.250(-.616 TO 1.116)	3.000 (-4.620 TO 10.620)
144	-0.405 (-2.038 TO 1.228)	0.667(-.422 TO 1.755)	1.500 (0.466 TO 2.534)
148	0.0 (0.0 TO 0.0)	1.000(1.000 TO 1.000)	1.333 (0.874 TO 1.793)
152	-0.288 (-1.442 TO 0.867)	0.750(-.116 TO 1.616)	1.333 (0.817 TO 1.850)
156	-0.693 (-2.693 TO 1.307)	0.500(-.500 TO 1.500)	2.500 (-0.970 TO 5.970)
160	-0.511 (-1.971 TO 0.950)	0.600(-.276 TO 1.476)	1.333 (0.757 TO 1.910)
164	0.0 (0.0 TO 0.0)	0.0 (0.0 TO 0.0)	2.000 (2.000 TO 2.000)
168	0.0 (0.0 TO 0.0)	0.0 (0.0 TO 0.0)	0.0 (0.0 TO 0.0)

TABLE OF CUMULATIVE TOTALS (THE A(I,J))

PEROMYSCUS   AREA 3   5 YR SLASH   HANEY

FEMALES

Column headers: 51 55 59 63 72 77 91 95 99 103 1C7 111 115 119 123 127 131 136 140 144 148 152 156 160 164 168

Row labels (top to bottom): 51 55 59 63 72 77 91 95 99 103 1C7 111 115 119 123 127 131 136 14C 144 148 152 156 16C 164

THE SUMS A(I,J)

THE SUMS N(I,J)

DISTRIBUTION OF RECAPTURES ACCORDING TO THE INTERVAL SINCE THEY WERE LAST CAPTURED (METHOD B GROUP).

PEROMYSCUS   AREA 3   5 YR SLASH   HANEY

FEMALES

WEEK OF LAST CAPTURE (rows) × WEEK OF CAPTURE (columns)

WEEK OF LAST CAPTURE	51	55	59	63	72	77	91	95	99	103	107	111	115	119	123	127	131	136	140	144	148	152	156	160	164	168
51	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
55	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
59	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
63	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
72	0	0	0	0	3	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
77	0	0	0	0	0	4	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
91	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
99	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
103	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
107	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
111	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
115	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
119	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
123	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
127	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
131	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
136	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
140	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
144	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
148	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
152	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
156	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
160	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
164	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

	51	55	59	63	72	77	91	95	99	103	107	111	115	119	123	127	131	136	140	144	148	152	156	160	164	168
TOTAL MARKED	0	1	2	3	1	3	4	4	1	5	5	5	9	7	6	7	1	5	2	1	2	1	1	1	1	1
TOTAL UNMARKED	1	1	1	1	6	5	2	1	6	5	5	2	4	3	1	2	1	1	1	1						
TOTAL CATCH	1	2	3	4	5	12	5	5	5	7	10	7	11	13	10	7	9	2	3	6	3	2	2	2	2	
TOTAL RELEASED	1	2	3	4	5	12	5	5	5	7	10	7	11	13	10	7	9	2	3	6	3	2	2	2	2	

POPULATION PARAMETERS ESTIMATED FROM MULTIPLE RECAPTURE DATA - JOLLYS STOCHASTIC MODEL

PEROMYSCUS AREA 3 5 YR SLASH HANEY

FEMALES

WEEK	ALPHA	M	N + 4 SE		PHI + 4 SE		B + 4 SE		LAMBDA + 4 SE	
			WEEK OF CAPTURE		WEEK OF CAPTURE					
51	0.0	0.0	0.0 +	0.0	1.000 +	0.0	0.0 +	0.0	0.0 +	0.0
55	0.5000	1.00	2.0 +	0.0	1.000 +	0.0	1.0 +	0.0	1.500 +	0.000
59	0.6667	2.00	3.0 +	0.0	1.000 +	0.0	1.0 +	0.0	1.333 +	0.000
63	0.7500	3.00	4.0 +	0.0	0.250 +	0.866	8.0 +	0.0	9.000 +	48.000
72	0.1111	1.00	9.0 +	3.5	0.333 +	0.629	9.0 +	0.0	4.000 +	2.083
77	0.2500	3.00	12.0 +	5.8	0.354 +	0.590	2.8 +	5.9	1.667 +	0.183
91	0.6000	4.25	7.1 +	5.8	0.607 +	0.977	0.7 +	6.4	1.103 +	0.071
95	0.8000	5.67	7.1 +	9.9	0.602 +	0.876	0.8 +	2.5	1.176 +	0.035
99	0.8000	4.00	5.0 +	6.7	0.480 +	1.109	14.4 +	51.4	7.000 +	36.340
103	0.1429	2.40	16.8 +	53.1	0.794 +	0.838	0.0 +	41.3	1.000 +	0.600
107	0.5000	6.67	13.3 +	14.7	0.669 +	0.746	2.0 +	9.3	1.225 +	0.087
111	0.7143	7.80	10.9 +	12.8	0.831 +	0.891	8.8 +	17.1	1.974 +	0.312
115	0.4545	8.14	17.9 +	21.7	0.636 +	0.580	1.6 +	10.9	1.140 +	0.075
119	0.6923	9.00	13.0 +	9.9	0.538 +	0.553	3.0 +	0.0	1.429 +	0.019
123	0.7000	7.00	10.0 +	8.9	0.717 +	0.601	1.2 +	2.1	1.167 +	0.008
127	0.8571	7.17	8.4 +	9.1	0.857 +	0.529	1.8 +	1.9	1.256 +	0.013
131	0.7778	7.00	9.0 +	8.4	1.000 +	2.811	9.0 +	54.3	2.000 +	1.832
136	0.5000	9.00	18.0 +	70.2	0.500 +	1.414	-3.0 +	25.3	0.667 +	0.227
140	0.8333	5.00	6.0 +	6.4	0.833 +	2.388	2.5 +	11.7	1.500 +	0.251
144	0.6667	5.00	7.5 +	23.8	0.500 +	1.944	2.3 +	16.2	1.600 +	1.294
148	0.5000	3.00	6.0 +	22.1	0.750 +	2.646	1.5 +	18.3	1.333 +	1.298
152	0.5000	3.00	6.0 +	22.1	0.500 +	1.414	0.0 +	8.0	1.000 +	0.444
156	0.6667	2.00	3.0 +	5.8	0.333 +	1.089	1.0 +	0.0	2.000 +	0.904
160	0.5000	1.00	2.0 +	3.8	0.500 +	1.414	1.0 +	0.0	2.000 +	0.726
164	0.5000	1.00	2.0 +	5.3	0.0 +	0.0	0.0 +	0.0	2.000 +	0.0
168	0.5000	0.0	0.0 +	0.0	0.0 +	0.0	0.0 +	0.0	0.0 +	0.0

WEEK OF LAST CAPTURE

ALPHA IS PROPRTION OF MARKED ANIMALS
M IS TOTAL MARKED POPULATION
N IS TOTAL POPULATION

PHI IS PROBABILITY OF SURVIVAL
B IS NUMBER OF NEW ANIMALS JOINING THE POPULATION
LAMBDA IS DILUTION RATE(AS DEFINED BY JOLLY)

STANDARDIZED 28-DAY RATES + 4 SE LIMITS

PEROMYSCUS AREA 3   5 YR SLASH   HANEY

FEMALES

WEEK	INST. DEATH RATE	SURVIVAL RATE	DILUTION RATE
51	0.0 (0.0 TO 0.0)	1.000(1.000 TO 1.000)	0.0 (0.0 TO 0.0)
55	0.0 (0.0 TO 0.0)	1.000(1.000 TO 1.000)	1.500 (1.499 TO 1.501)
59	0.0 (0.0 TO 0.0)	1.000(1.000 TO 1.000)	1.333 (1.332 TO 1.334)
63	-0.616 (-2.156 TO 0.923)	0.540(-.291 TO 1.371)	2.655 (-0.979 TO 6.289)
72	-0.879 (-2.387 TO 0.630)	0.415(-.211 TO 1.042)	3.031 (-0.469 TO 6.532)
77	-0.297 (-0.773 TO 0.180)	0.743(0.389 TO 1.097)	1.157 (0.818 TO 1.496)
91	-0.098 (-1.176 TO 0.980)	0.907(-.071 TO 1.884)	1.103 (0.034 TO 2.172)
95	-0.511 (-1.971 TO 0.950)	0.600(-.276 TO 1.476)	1.176 (0.431 TO 1.922)
99	-0.734 (-3.043 TO 1.575)	0.480(-.629 TO 1.589)	7.000 (***** TO 31.113)
103	-0.231 (-1.287 TO 0.824)	0.794(-.044 TO 1.631)	1.000 (-2.098 TO 4.098)
107	-0.403 (-1.518 TO 0.713)	0.669(-.077 TO 1.414)	1.225 (-.043 TO 2.407)
111	-0.185 (-1.258 TO 0.887)	0.831(-.060 TO 1.722)	1.974 (-0.259 TO 4.208)
115	-0.452 (-1.364 TO 0.460)	0.636(0.056 TO 1.217)	1.140 (0.046 TO 2.235)
119	-0.619 (-1.646 TO 0.408)	0.538(-.015 TO 1.092)	1.429 (0.881 TO 1.976)
123	-0.333 (-1.172 TO 0.505)	0.717(0.116 TO 1.319)	1.167 (0.814 TO 1.519)
127	-0.154 (-0.771 TO 0.463)	0.857(0.328 TO 1.386)	1.256 (0.807 TO 1.704)
131	0.0 (-2.249 TO 2.249)	1.000(***** TO 3.249)	1.741 (-2.030 TO 5.512)
136	-0.693 (-3.522 TO 2.135)	0.500(-.914 TO 1.914)	0.667 (-1.240 TO 2.573)
140	-0.182 (-3.048 TO 2.684)	0.833(***** TO 3.222)	1.500 (-0.506 TO 3.506)
144	-0.693 (-4.580 TO 3.194)	0.500(***** TO 2.444)	1.600 (-2.950 TO 6.150)
148	-0.288 (-3.815 TO 3.240)	0.750(***** TO 3.356)	1.333 (-3.224 TO 5.890)
152	-0.693 (-3.522 TO 2.135)	0.500(-.914 TO 1.914)	1.000 (-1.667 TO 3.667)
156	-1.099 (-4.365 TO 2.167)	0.333(-.755 TO 1.422)	2.000 (-1.804 TO 5.804)
160	-0.693 (-3.522 TO 2.135)	0.500(-.914 TO 1.914)	2.000 (-1.408 TO 5.408)
164	0.0 (0.0 TO 0.0)	0.0 (0.0 TO 0.0)	2.000 (2.000 TO 2.000)
168	0.0 (0.0 TO 0.0)	0.0 (0.0 TO 0.0)	0.0 (0.0 TO 0.0)

APPENDIX 4

Mean Probability of Survival and Variance (28 day ϕ)

ℓ_i = number of weeks in sample

s = number of sample periods

$$\overline{\phi} = \left[\prod_{i=1}^{s} \phi_i \right]^{\dfrac{4}{\sum_{i=1}^{s} \ell_i}}$$

$$V(\overline{\phi}) = \left(\overline{\phi} \; \dfrac{4}{\sum_{i=1}^{s} \ell_i} \right)^2 \left[\sum_{i=1}^{s} \dfrac{V\phi_i}{\phi_i^2} + \sum_{i=2}^{s} \dfrac{2 \; \text{Cov} \left(\phi_{i-1}, \; \phi_i \right)}{\phi_{i-1} \; \phi_i} \right]$$

where $\text{Cov} \left(\hat{\phi}_{i-1}, \; \phi_i \right) = - \phi_{i-1} \; \phi_i \left[\dfrac{M_i - n_i}{M_i} \left(\dfrac{1}{R_i} - \dfrac{1}{S_i} \right) \right]$

M_i = total number of marked animals in the population at time i.

N_i = number of marked animals in the i th sample.

R_i = the number of the S_i animals released from the i th sample which are caught subsequently.

S_i = the number of animals released marked from the i th sample.

Test Criteria

$$\text{T.C.} = \dfrac{\overline{N} - \overline{N}_y}{\sqrt{\text{Var} \; \overline{N}_x + \text{Var} \; \overline{N}_y}}$$

CURRICULUM VITAE

Bruce Gordon Petticrew

PERSONAL HISTORY

    Place of birth: Victoria, British Columbia
    Date of birth: March 9, 1945
    Marital Status: Married

EDUCATIONAL BACKGROUND

    Graduated from Oak Bay Senior Secondary, 1964

    <u>Degrees</u>

      B.Sc. (Mathematics and Zoology) May 1968.

AWARDS

    British Columbia Government Scholarships 1966-67 and 1967-68
    Simon Fraser University President's Research Grant, Spring 1970

TEACHING EXPERIENCE

    Teaching Assistant, Simon Fraser University: BISC 101-BISC 102,
    Introduction to Biology; BISC 316, Vertebrate Biology;
    BISC 407, Population Dynamics.

GRADUATE COURSES TAKEN

    BISC 843 - Population Processes
    BISC 869 - Special Topics II: Advanced Ecology
    BISC 836 - Vertebrate Reproductive Ecology
    BISC 879 - Special Topics III: Modern Forestry Practices
    BISC 806 - Adaption and Adaptability.

MEMBERSHIP IN PROFESSIONAL ORGÁNIZATIONS

    The Canadian Society of Zoology

PUBLICATIONS

    Petticrew, B.G. and R.M.F.S. Sadleir. (1970) The use of index
        trap lines to estimate population numbers of deermice
        <u>Peromyscus</u> <u>maniculatus</u> in a forest environment in British
        Columbia. Can. J. Zool. <u>48</u>:385-389.