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**DETERMINANTS OF HOME RANGE IN THE
DEER MOUSE, *PEROMYSCUS LEUCOPUS***

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ABSTRACT: The movements of mice on the islands of Lake Opinicon, Ontario, were studied by means of smoked paper tracking, supplemented by livetrapping. The mice had fairly stable home ranges, usually linear in outline. Estimated minimum home-range areas ranged from 0.03 to 2.31 acres, but the data are inadequate to show any correlation of area with age or sex. The mice usually seemed to use their home ranges heterogeneously, leaving many more records at some stations and many fewer at others than would be expected from random movement, but track and trap data do not permit a satisfactory analysis of patterns of home-range utilization. Location and size of home range were influenced by the physical environment, exploration, food supply, social interaction, and habit. Mice accustomed to using an artificial food supply often shifted their home ranges when this supply was moved. Evidence of the role of social interaction included: 1) There was much overlap of home ranges, but mice of the same sex and generation tended to occupy mutually exclusive ranges. 2) Home ranges tended to be larger in sparse populations, apparently not as a result of poor food supply. 3) The removal of one or more mice often was followed by the movement of other mice into the vacated home ranges. The role of habit is shown by the fact that some mice remained in the same home range even after neighboring mice were removed, and by the lack of correlation between numbers of records at the stations on one island in 2 different years. Home range benefits the species by providing a more stable environment for each mouse, thereby promoting survival and facilitating the self-regulation of breeding by the population.

INTRODUCTION

Animals of many species do not wander at random, but confine their activities to limited areas that they visit repeatedly. Each individual or social group becomes familiar with its own area—the physical structure, resources, and dangers, and the presence of other members or groups of the same species. This familiarity is gained as a result of exploration, usually early in life, and



FIGURE 1. Deciduous forest on Hoffman Island. Note undergrowth, leaf litter, and milk carton track shelter at stake marking a station.

is renewed and revised by continual reexploration as long as the area is occupied (Sheppe, 1966a). This familiar area is more than just a satisfactory place to live—the animal has a positive relationship to this specific area, as shown by the frequency with which animals return home when released at distant points.

The nature and function of this home area vary widely in different groups of animals. It may be individual or communal, large or small, permanent or seasonal, used exclusively by one individual or group or shared by several. All of the animal's activities may take place in this area, or the animal may have to leave at times for some purpose such as finding a mate.

One of the early studies of this phenomenon in small mammals was Burt's (1940) study of the movements of *Peromyscus leucopus*. He found that each mouse was confined to a limited area during its adult life, and called this area the mouse's "home range," which he defined as "the area, usually around a home site, over which the animal normally travels in search of food" (Burt, 1943).

Since then many other workers have studied home ranges of small mammals, usually using methods and concepts similar to Burt's. A somewhat different concept of home range was presented by Hayne (1949) and further elaborated by Calhoun and Casby (1958). They conceive of home range as delimited not by fixed lines but by statistical zones of decreasing probability of occurrence.

Home-range studies of small mammals have suffered from the lack of suitable methods of observing the animals. It usually is not possible to observe them directly and almost all of our knowledge has been obtained by methods that present very limited information and that may interfere unduly with the phenomenon being studied (Sheppe, 1966b). The most widely used method has been the repeated livetrapping and release of marked animals. In the present study the movements of the mice were detected primarily by the use of smoked paper tracking (Justice, 1961). This method provides more data than trapping and does not interfere with the movements of the mice, but is affected even more by behavioral variability (Sheppe, 1965a).

The numerous studies of home range in *Peromyscus* probably have given a fairly accurate picture of where the mice travel, but have revealed little of the nature and pattern of use of various parts of the ranges, or of the causal mechanisms that determine where a mouse moves. The main objective of this study was to clarify the last question, primarily by means of experimental manipulation of mouse populations or of their environment. Because of the limitations of the techniques used and the variability of the phenomena studied the results reported below illustrate the role of various factors, but do not show the relative importance of each.

METHODS

This work was done on the islands of Lake Opinicon, in southeastern Ontario, during the periods May 23 to September 1, 1963 and May 23 to October 3, 1964. At times traps were set on the mainland adjacent to the islands. The islands and their mouse populations have been described elsewhere (Sheppe, 1965b). Most of the area is covered by mature second-growth deciduous forest (fig. 1). The animal studied was *Peromyscus leucopus noveboracensis* (Fischer). Some of the populations were natural, others introduced. Some colonists left their islands by swimming soon after they had been released (Sheppe, 1965c). Often the mice that remained soon bred, resulting in unusually dense populations (Sheppe, 1965d). Adult mice had been born the previous year and were in adult pelage. Young mice had been born 1 to 5 months earlier and were in juvenal or subadult pelage. Additional data on the islands and populations discussed below are given in table 1.

Home ranges on most of the islands were studied primarily by smoked paper tracking, supplemented by occasional livetrapping. In the tracking technique each mouse is marked distinctively by removing one or more toes. The track shelters were quart cardboard milk cartons, sometimes supplemented by large fruit-juice cans. Holes were cut in both ends and the shelters were laid on their sides on the ground. A smoked card was put in each shelter and when a mouse walked through he left tracks that usually could be identified by noting which toes were missing. Trapping was with small Sherman traps

TABLE 1. *Characteristics of the islands and their mouse populations. All of the introduced mice were sexually mature. The natural populations included both mature and immature mice, except on Sheep Island where the immatures had been removed.*

ISLAND	SIZE (ACRES)	NO. OF STATIONS	HABITATS	POPULATION
Cow	16.7	291	Mostly deciduous forest, some good rock cover.	1963: 40, 1964: 10 (natural)
Eight Acre	37.6	—	Mature deciduous forest with good rock cover (in section studied).	— (natural)
Hoffman	6.5	107	Deciduous forest, some rock and log cover.	1963: 50, 1964: 6 (natural)
Hump	0.61	70	Bare rock, low herbs and lichens, some small trees and shrubs, much rock cover, no logs.	1963: 5 ♂♂, 5 ♀♀ (introduced) 1964: 5 ♂♂, 5 ♀♀ (introduced)
Loon's Nest	0.53	37	Mixed forest, much blueberry, some good rock cover, few logs.	5 ♂♂, 5 ♀♀ (introduced)
Sheep	3.9	57	Mostly open mixed forest with sedge ground cover, good rock and log cover in places.	3 ♂♂, 5 ♀♀ (natural)

baited with whole oats, although large Sherman traps with cotton were occasionally used in cold weather. Most of the Cow Island and all of the Eight Acre Island data are from trapping. Trap and track stations were set on a rectangular grid, 25 feet (Hump, Loon's Nest) or 50 feet (Cow, Hoffman, Sheep) apart. On Hump there were 44 stations on the grid and 26 at other locations. There was no grid on Eight Acre.

Peromyscus is almost entirely nocturnal, and records were kept by night. Night 1 for natural populations was the first night traps were set, for introduced populations the first night the population was on the island. Traps were checked each morning, cards daily or on alternate days.

The number of records of each mouse ranged from 1 to almost 300. Most of the accounts below are based on 10 or more records per mouse. For many of the mice the number of records is greater than in previous studies, giving an unusually reliable picture of the movements of the mice, but there were two complicating factors that necessitate caution in interpreting the results. The mice behaved very differently for 1 or more nights after being trapped than at other times, and sometimes they wandered far outside their previous ranges (Sheppe, 1966b). The other complicating factor was that the mice entered the track shelters to explore them and this exploration was less con-

sistent than the combination of exploration and food-seeking involved in trapping. The results reported below do not seem to have been affected significantly by either of these factors.

An artificial feeder was used on one island to determine the effect of a food supply on the movements of the mice. It consisted of a platform on which was mounted a cylindrical food hopper of hardware cloth. The hopper was filled with whole oats, which the mice removed through the hardware cloth. It was surrounded by a larger cylinder of sheet metal with partitions forming four separate feeding compartments, so that four mice could feed simultaneously without coming in contact. Access to these compartments was through holes in the sheet metal. Smoked cards were placed in each compartment, on the platform outside, and in shelters around the feeder to record the presence of the mice.

RESULTS

I. DESCRIPTION OF HOME RANGE.

Shape.

Stumpf and Mohr (1962) have pointed out that the home ranges of various small mammals and other vertebrates often are linear rather than circular. Home ranges of *Microtus* and *Reithrodontomys* that they observed averaged about 2.8 times as long as wide. In the present study also most home ranges were distinctly linear. During one 5-day period on Hump Island the ratio, length/width, ranged from 2.1 to 4.0 ($\bar{x} = 2.9$) for the seven mice. Several weeks later the ratios for the four remaining mice were 1.5 to 3.5 ($\bar{x} = 2.2$). Some of this linearity was imposed by the shape of the island, but in the first period none of the mice were recorded over the full width of the island.

Many of the mice on Cow Island in 1963 had ranges that were restricted little if any by the lake. In 12 instances mice left 5 to 13 records during periods of 3 to 16 nights and apparently had stable home ranges. The length/width ratio for these mice ranged from 1.3 to 5.3 ($\bar{x} = 3.0$). Five mice on Hoffman Island in 1963 had ratios of 1.5 to 3.0 ($\bar{x} = 2.1$).

Often the shape of the home range was associated with obvious habitat variables. Some of the linear ranges on Cow were in areas of linear rock outcrops, like the ranges of *P. boylii* observed by Brown (1964). Most of the long narrow ranges observed on Hump were along the cliffs on either side of the island. The most compact ranges were at the southern tip of the island, an area of broken rock isolated from other areas of suitable habitat by a long stretch of unbroken rock.

Sometimes mice seemed to use discontinuous ranges. Several mice were recorded for short periods from the areas of broken rock on both ends of Hump, but not from the area between. They apparently used this area only in transit.

The most striking example of such discontinuity was that of an adult male that was the only resident of Island 14 in 1964. He is known to have crossed to the mainland at least six times in a 2-month period, and probably crossed much more often. The island is 160 feet from the mainland and connected to it by a cattail (*Typha* spp.) marsh, and the mouse was recorded once from the center of this marsh. The marsh had a bottom of wet black muck and the mouse probably was able to cross getting only his feet wet. He was recorded over all of the 0.8-acre island, but apparently used only a small area on the mainland.

Size.

Size is one of the most important of home-range data, but it usually is not possible to get a very meaningful estimate of it. One difficulty is that the concept of home range is complex and no single measure of home-range size can serve all purposes. Social interactions may be prominent in parts of a range and feeding in other parts, and studies of bioenergetics will be concerned only with the latter. Specification of the nature and intensity of use of each part of the range is necessary for a meaningful statement on range size. Such information is never really available, because of the inadequacy of our techniques for observing the mice. Trap and track data are both qualitatively and quantitatively inadequate.

Another major difficulty in characterizing home ranges is their great variability. Size, shape, and patterns of use vary widely among different mice, and each mouse's home range presumably is constantly changing to some extent. Because of this variability statistical analysis may be misleading.

In spite of these difficulties, crude estimates of home-range size often are better than none. The home-range sizes below were estimated by the minimum area method, in which a line is drawn connecting the outermost stations where a mouse was recorded and the area within determined by use of a planimeter. The outermost stations were chosen subjectively, based on number of records and habitat type. All estimates are based on at least five trap or track records made during periods when the mouse apparently was occupying a stable home range. It is probable that all of these estimates are smaller than the area actually used by the mice.

There are data suitable for estimating home-range size of only a few mice in the natural populations. Estimates of areas of apparently stable home ranges of 13 mice over various lengths of time on Cow Island ranged from 0.03 to 0.75 ($\bar{x} = 0.37$) acre. Both the largest and smallest estimates were for adult females, both based on seven records. There is no indication of age or sex differences. A subadult male on Hoffman Island in 1963 was recorded over 0.72 acre, an adult and two subadults in 1964 over 2.18, 2.31, and 1.68 acres, respectively.

The movements of all of the mice in the introduced colony on Hump Island were restricted on some sides by water, but apparently the small size of the island did not directly limit home-range size for most of the mice. The area bounded by the outermost stations was 0.57 acre, which is larger than most of the home-range estimates on Cow. No mouse on Hump was recorded over all of this area during any one period of home-range stability, and most of them seemed to restrict their movements to less than half of the island.

During the 3rd week that the colony was on Hump Island in 1964 the two males had ranges of 0.33 and 0.35 acre, the five females ranges of 0.17 to 0.24 ($\bar{x} = 0.20$) acre. The weekly estimates of home-range size for ♂ 830 for 14 weeks (excluding 3 weeks when there were few records) ranged from 0.31 to 0.45 ($\bar{x} = 0.39$) acre. These estimates do not adequately reflect the apparent changes in his home range mentioned below.

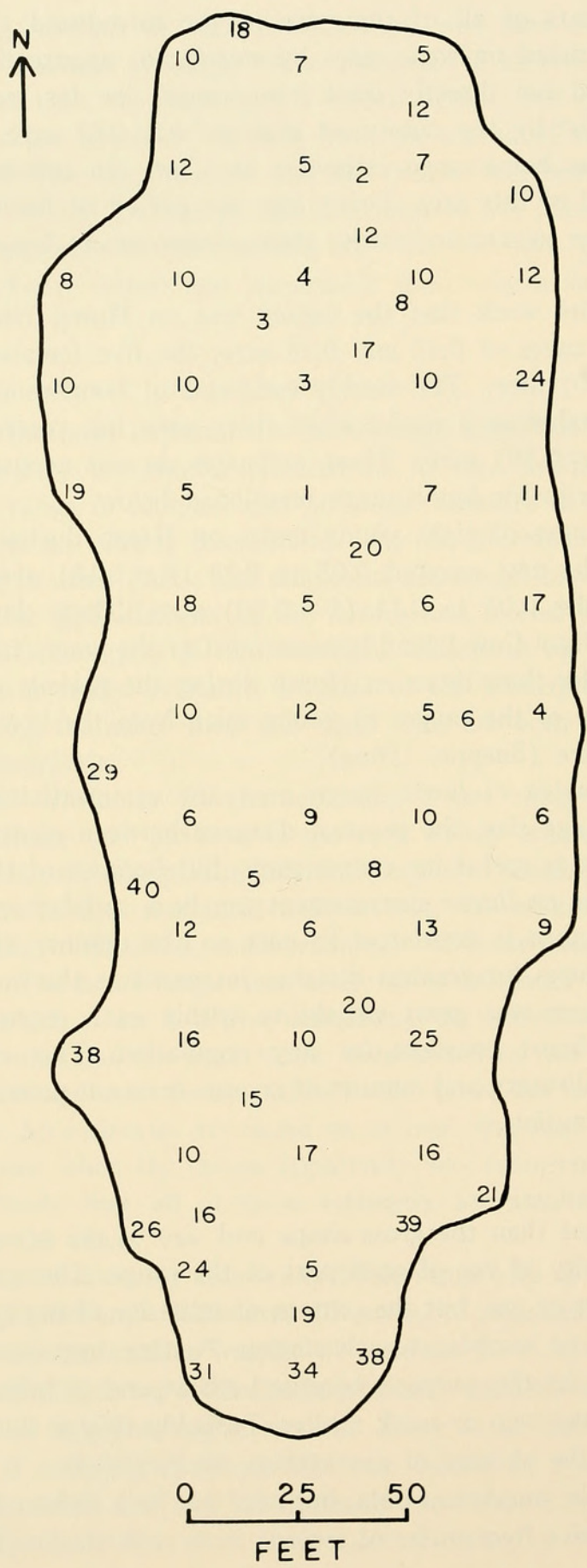
The home ranges of eight young males on Hump during a week shortly after they left the nest covered 0.02 to 0.24 ($\bar{x} = 0.13$) acre, the ranges of four young females 0.04 to 0.14 ($\bar{x} = 0.10$) acre. These data are not comparable to those from Cow Island because most of the young mice on Cow were several weeks older than those on Hump during the periods in question. The gradual expansion of the ranges of young mice from the home nest has been described elsewhere (Sheppe, 1966a).

Because estimates of home range area are so unsatisfactory, a simpler index of home-range size, the greatest distance between records, will be used below. This index is useful for comparisons, but because of the variability of home-range shapes no linear measurement can be a satisfactory index of area. The greatest distance is dependent in part on the number of records. Mean and minimum figures for greatest distance increased as the number of records increased, but there was great variability within each record class and the maximum was almost constant for any population. This complex relation between greatest distance and number of records makes it necessary to interpret such data with caution.

Pattern of use.

More important than the gross shape and size of the home range are the nature and intensity of use of each part of the range. There are virtually no data on the nature of use, but the pattern of intensity of use can be estimated from the number of records at each station. Neither trap nor track data are really satisfactory for this purpose, because both depend on behavioral responses by the mouse to the trap or track shelter. Probably only a small fraction of a mouse's visits to the vicinity of any station are recorded.

This reduces the number of data, but need not be a serious drawback unless it affects the relative frequencies of records from each station. It is not known



whether there is such a bias in either trap or track data, but it is probable that there is some bias in both. Trapping restricts the movements of the mice, and after they are released their activity is increased and their pattern of movement may be affected (Sheppe, 1966b). Tracking does not have these drawbacks, but it is dependent on the exploratory behavior of the mice, and this declines over a period of time (Sheppe, 1966a).

A mouse may acquire the habit of visiting one trap, resulting in an artificial concentration of records at that station. If mice react to track shelters as a class of objects this will create a bias in favor of the first few shelters that they encounter each night, but if they react to each shelter as a unique object this will create a bias toward uniform numbers of records from all stations. The results of the present study suggest that none of these possible biases are great enough to invalidate the results, and the track data will be analyzed with the tentative assumption that they constitute an unbiased record of the relative frequency with which a mouse visits the vicinity of each station.

If a mouse moves through its home range at random, the number of records from each station should fit a random discontinuous distribution such as the Poisson. If the mouse covers its home range uniformly, one record at a station will reduce the probability that another record will be made there and the total number of records from each station will diverge from the Poisson in the direction of greater homogeneity. If the mouse tends to visit some parts of its home range more than others, each record will increase the probability of additional records at that station and the total number will diverge in the direction of heterogeneity. This is the result that would ordinarily be expected, because of habitat heterogeneity and because of habit formation by the mouse.

Collectively the mice showed a marked heterogeneity of use of the islands. The number of track records from each station on Hump Island ranged from one to 40 ($\bar{x} = 13.56$) in 1963 (fig. 2). Figure 3 shows that this is a far greater degree of heterogeneity than would be expected if the mice had left records at random. The mean observed number of stations has been plotted for each group of five record classes and the expected number calculated for selected record classes. Complete homogeneity would be shown by a vertical line at $x = 13.56$, extending from the abscissa to $y = 70$. The Poisson distribution approaches this far more closely than does the observed distribution. There were many more stations with few records and with many records than would have been expected, and fewer stations with an intermediate number of records.

Individual mice also usually showed such heterogeneity of use of their home ranges. The following examples are based on periods when the mice seemed

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FIGURE 2. Number of track records from each station on Hump Island in 1963.

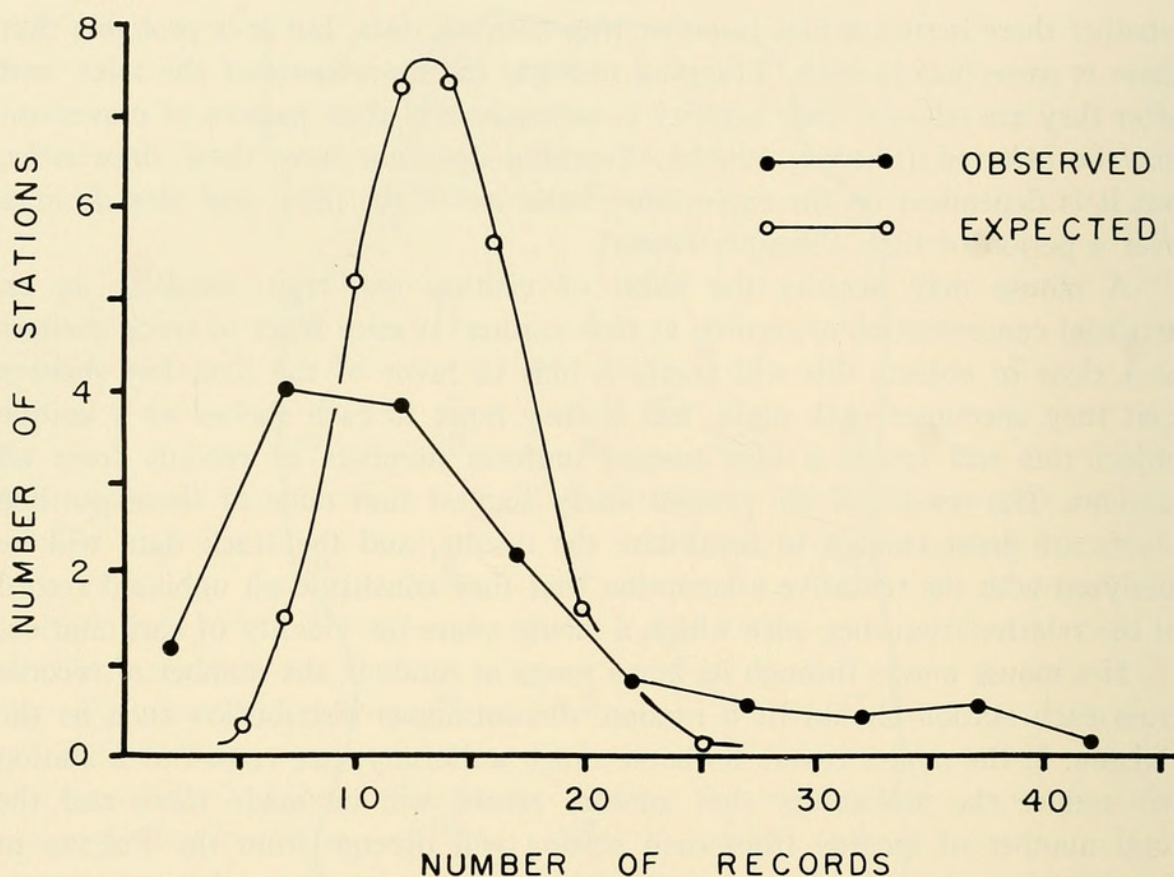


FIGURE 3. Frequency distribution of number of stations with each number of track records, from figure 2. The expected number is calculated from the Poisson equation.

to have stable home ranges. There were no gross changes during these periods, but presumably there were changes in pattern of use that the data are not adequate to show.

Figure 4 shows the number of records left by ♂ 830 at each station on Hump Island during a 14-night period. He left 79 records, from 0 to 6 ($\bar{x} = 1.13$) at each station. The number of stations with no records and with four or more records is greater than expected, the number with one to three records less ($P < 0.02$).

This mouse was assumed to use the entire island, but usually a mouse uses only a small part of the area available to him and there is no satisfactory way of determining the total number of stations in his home range. In such cases the first record at each station can be used to define the home range, and the expected distribution calculated on the basis of subsequent records only. A station with no records is not considered part of the home range, a station with one record is credited with zero records, etc.

During a period of 20 nights ♀ 807 left many records on the south tip of Hump Island, fewer toward the center, and one isolated record near the north end. This distribution deviated strongly ($P < 0.01$) from the expected calcu-

lated as described above. During a later period of 9 nights she was recorded only on the north end of the island and left records more or less at random ($P > 0.20$).

Even when the difference between expected and observed distributions was not statistically significant there usually was a tendency toward heterogeneity. This heterogeneity probably reflects a real difference in the frequency with which track shelters were encountered, but this may not be an accurate indication of the amount of time a mouse spent in the grid square centered around each shelter. The shelter may have been in the most or the least frequently visited spot in that square. Often a grid station had few records while an off-grid station a few feet away had many.

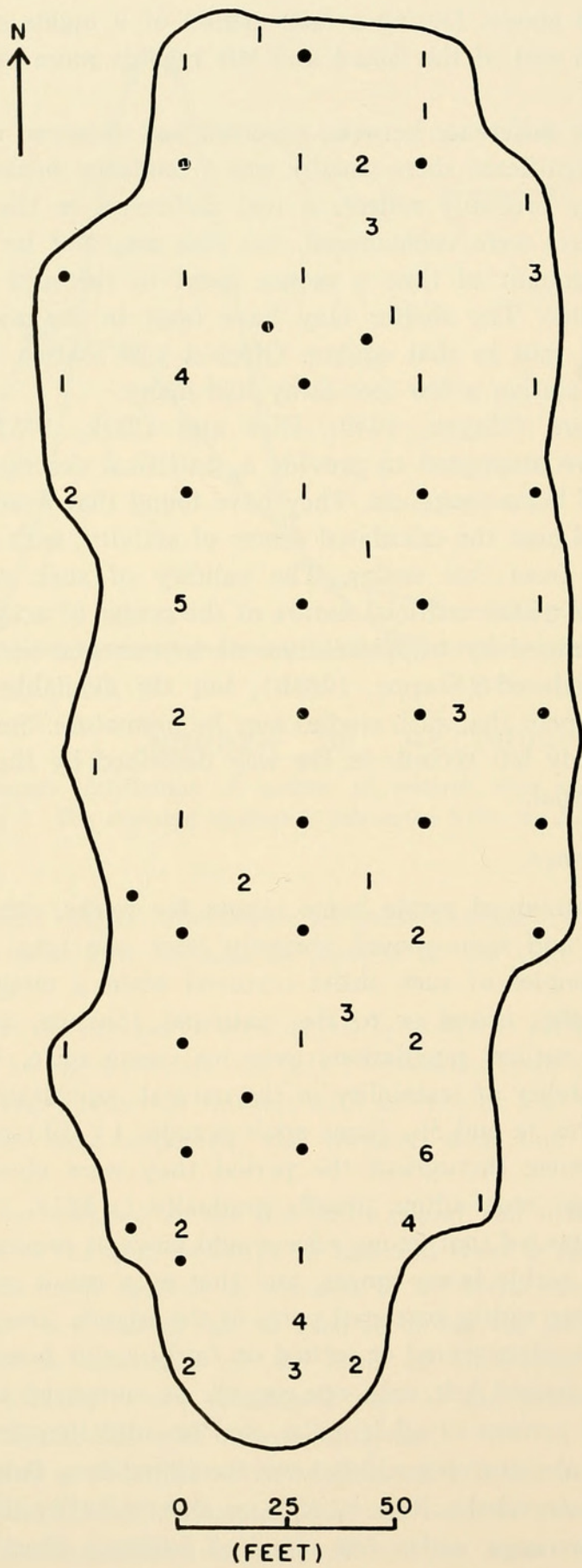
Various workers (Hayne, 1949; Dice and Clark, 1953; Calhoun and Casby, 1958) have attempted to provide a statistical description of the geographic pattern of home-range use. They have found that livetrapped records tend to be concentrated near the calculated center of activity, with fewer records at greater distances from this center. The validity of such studies has been questioned because of the artificial nature of the center of activity and because of possible bias caused by trap inhibition of movements. Such bias may not be as great as believed (Sheppe, 1966b), but the available data on mouse movements are so poor that such studies may be premature. Sometimes a mouse in the present study left records in the way described by the above workers, but this was unusual.

Shifts in home range.

Some mice maintained stable home ranges for weeks, others shifted their ranges gradually, and some moved abruptly from one area to another. The most striking examples of such shifts occurred when a mouse emigrated by swimming to another island or to the mainland (Sheppe, 1965c). All such emigrations from natural populations were by young mice. Various patterns of home-range stability or instability in the natural population on Cow Island are shown in figures 5a and 5b. Some adult females ($\text{♀} 401$) maintained essentially the same range throughout the period they were observed, but adult males shifted ranges more often, usually gradually ($\text{♂} 421$).

It had been expected that young mice would move at random for some time before settling on stable home ranges, and that as a result many young mice would be found over widely scattered parts of the islands. Instead, most young mice either quickly disappeared or settled on fairly stable home ranges. Of the young males, 46 percent left only one record, as compared to 21 percent of young females, 18 percent of adult males, and no adult females.

Some young males traveled widely over the island in a short time and then disappeared, some traveled a long ($\text{♂} 584$) or short ($\text{♂} 476$) distance and then settled on a stable range, and a few remained within a short distance of the



place where first trapped (δ 608). Young females usually did not range as widely as young males. Sometimes a young mouse moved through a relatively large area at first and later established a more restricted range within this area.

All eight of the mice that survived the winter of 1963–1964 on Cow had originally been tagged on the south end, but by the following spring they were dispersed all over the island. Some examples of these shifts are shown in figures 5a and 5b (δ 426, δ 584, ♀ 857).

If home ranges are stable, the distance between successive records should not be influenced by the interval between records. Increasing distance with increasing interval should indicate shifting patterns of movement. Among adult males on Cow there was great variability, but the distances between records tended to be greater at longer intervals, indicating some shifting of ranges. The mean distance for intervals of 1 or 2 nights was about 145 feet, for 3 or more nights about 200 to 225 feet. The maximum and mean usually were greater for young than for adults, but the data are not adequate to show that the difference is greater at longer intervals.

At intervals of more than 1 night the maximum and mean for adult females was consistently less than for adult males, and there was no apparent increase at longer intervals. The maximum and mean usually were greater for young females than for adults, but there is no evidence that this difference increased with interval.

Some mice in the experimental colonies had stable home ranges, but in general the mice in these colonies tended to have less stable ranges than mice in natural populations, even when the colonies were not being manipulated. As examples of stability, two females on Hump Island established home ranges on the south end after the first few nights. Thereafter their ranges expanded or contracted somewhat but they were never recorded as far north as the middle of the island.

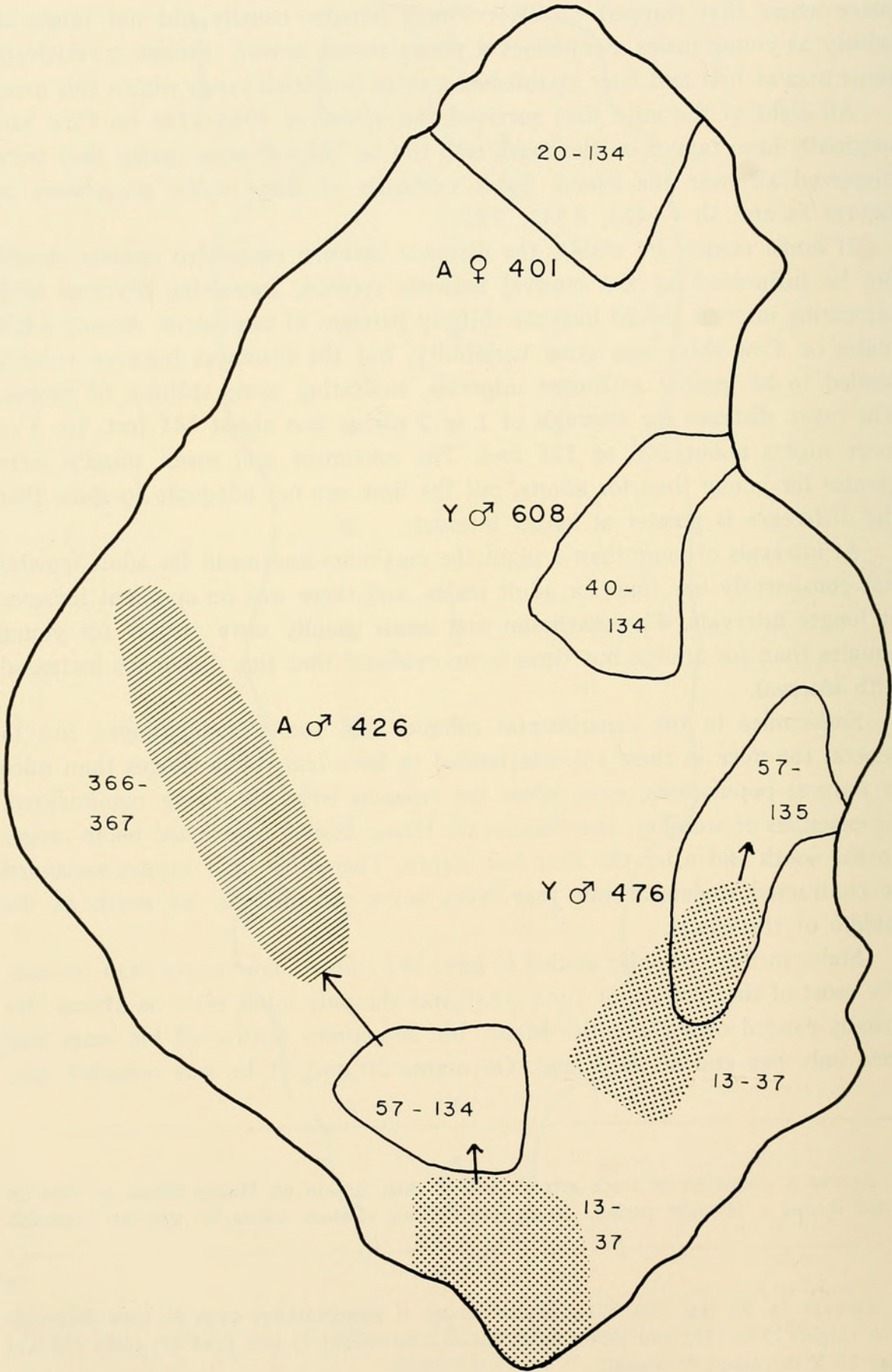
Males in these colonies tended to have less stable home ranges than females. For most of the summer of 1964 δ 830 was the only adult male on Hump. He usually ranged over the entire island, but sometimes contracted his range and used only one end of the island. On nights 20 and 21 he was recorded only

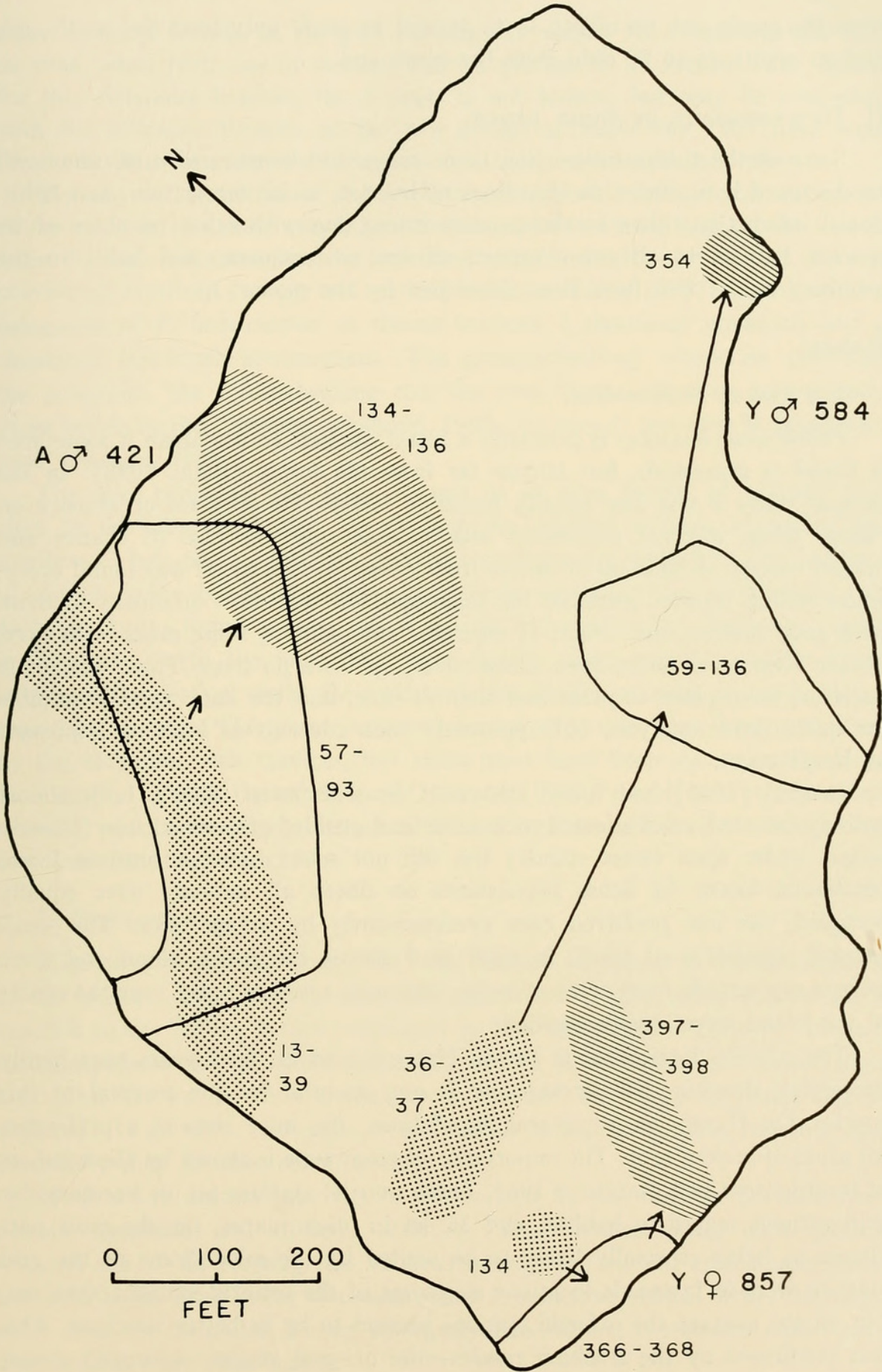
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FIGURE 4. Number of track records left at each station on Hump Island in 1964 by δ 830 during a 14-night period. Solid dots indicate stations where he was not recorded.

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FIGURES 5a, 5b (pp. 390, 391). Home ranges of representative mice on Cow Island in 1963 (nights 13 to 136) and 1964 (nights 354 to 429). Night 13 was June 13; night 354 was May 25. Y = young; A = adult.





from the south end, on nights 34 to 36 and 39 to 42 only from the north end, and on nights 55 to 70 only from the south end.

II. DETERMINANTS OF HOME RANGE.

Some of the things influencing home range and home-range utilization will be discussed here, under the headings of habitat, social interaction, and habit. Social interaction refers to the mouse's interaction with other members of its species, habitat to all other aspects of the environment, and habit to the arbitrary habits that have been developed by the mouse.

Habitat.

1. *Physical environment.*

Peromyscus leucopus is primarily a forest dweller. In Michigan it sometimes is found in grasslands, but seldom far from the forest (Blair, 1948). In the present study it was also usually found in forests. Its presence or absence on islands often was not correlated with habitat type, because of chance and limited variety of habitats to choose from (Sheppe, 1965b). It was found everywhere within forested areas on the mainland, but was most abundant in those with good broken rock cover. It was also abundant in some areas with good broken rock cover under open shrub cover, but with no trees. There was much variation from place to place and time to time, and the data are not suitable for quantitative analysis, but apparently rock cover is at least as important as forest cover.

Bendell (1961) had found that on Cow and Sheep islands, both almost entirely forested, mice selected rock cover and avoided grassform cover (mostly sedges under open forest stands) but did not select between hardwood and coniferous forest. In dense populations on Sheep all habitats were equally occupied, the less preferred ones predominantly by young mice. The small natural population of adults in 1964 used almost the entire island and there were many records from areas of sedge, but some areas of sedge near the center of the island were largely avoided.

The colonies introduced to barren Hump Island in the 2 years were highly successful, showing that forest cover is not essential for the survival of this species. On Hump, as in natural populations, the mice showed a preference for areas of broken rock. The importance of cover type is shown by the numbers of records from each station in 1963. There were 44 stations set on a rectangular grid without regard to habitat, and 26 set in other places, for the most part chosen as being especially likely to be visited by the mice. Some of the grid stations were in favorable locations and some of the off-grid stations were not, but on the average the off-grid stations seemed to be in better locations. This was confirmed by the tracking results—the off-grid stations averaged almost

twice as many records as the grid stations (19 versus 10). This was not true in 1964, when both sets of stations had an average of 20 records. The reason for this difference between the 2 years is not known, but may be connected with the different histories of the two groups of mice—the 1963 mice were caught in the wild while the 1964 mice had been born in the laboratory.

The physical structure of the environment probably affects the occurrence of the mice in two main ways, by providing proper visual and tactile stimuli when the mice are active, and by providing suitable crevices for nesting. Forests provide an overhead canopy and vertical surfaces. Harris (1952) permitted two subspecies of *P. maniculatus* to choose between a simulated grassland and a simulated tree-trunk environment. The prairie-dwelling subspecies preferred the grassland, the forest-dwelling one the tree trunks. Norway rats usually move beside vertical surfaces (Calhoun, 1963), as does *P. leucopus* in laboratory pens (Sheppe, 1966c).

The mice probably would not remain in an area devoid of suitable nest sites. In the laboratory they squeeze into the smallest crevices available. The numbers of hole-nesting birds on an area sometimes are limited by the numbers of suitable holes, and it is possible that this is sometimes true of the mice too. Jackson (1961) found a dense population of *P. leucopus* in a limestone ravine in Wisconsin, with the mice living one family above another on the many ledges on the vertical walls. He estimated the density of mice as much higher than 100 per acre. This great concentration of mice may have been permitted by the abundant rock crevices, but there must have been an unusually large food supply too. On the other hand, Howard (1949) found that supplying an excess of nest boxes did not attract additional representatives of *P. maniculatus bairdi* to his study area.

2. Exploration.

Mice have innate (Wecker, 1963) and learned responses to various features of the habitat—they tend to approach some features and avoid others. Their reaction to any feature is also influenced by how familiar it is (Sheppe, 1966a). Strange objects tend to evoke neophobia and be avoided, whereas objects that are unfamiliar but not new enough to be avoided will evoke neophilia and be explored. As an object becomes more familiar it will evoke less response and eventually may be ignored altogether.

Much of an animal's activity is determined by the balance between neophobia, neophilia, and stimulus satiation. This balance varies with species, sex, and age. Wild Norway rats (*Rattus norvegicus*) exhibit strong neophobia, but wild house mice (*Mus musculus*) and *P. leucopus* exhibit little. All three show clear-cut neophilia. Young laboratory rats explore more than older ones, and females more than males.

In the present study the exploratory behavior of the mice was shown most clearly by the large number of records in novel track shelters on the first night they were put out. Juice-can shelters were placed within a foot of the milk-carton shelters that had been present for some time on five islands. Invariably there were far more records in the cans than in the cartons the next day, but thereafter the number of records in cans dropped sharply and eventually was no greater than the number in cartons. The mice seem to enter the shelters to explore them, so that the number of records is an indication of the amount of exploration.

This exploration of unfamiliar objects shows that the mice have a good knowledge of their home ranges. This knowledge is gained initially by exploration and apparently is maintained by repeated reexploration. The physical features of a mouse's home range are constantly changing (leaf fall, snow cover, growth of vegetation) and the mouse probably finds some new object or condition to explore every night.

Since a mouse explores unfamiliar objects it might seem that he would continually explore farther and farther from the center of his home range, because everything out there is unfamiliar. This does not necessarily follow, even from the point of view of exploratory behavior, because this and other studies have shown that unfamiliar objects elicit exploration much more if they are in a place that is familiar to the animal. The animal's attention is aroused by change.

3. *Food supply.*

A satisfactory home range necessarily includes an adequate food supply. *Peromyscus* eats primarily seeds, and lesser quantities of fruits and invertebrates. The occurrence of these things varies greatly with the season, and a mouse's movement patterns can be expected to vary accordingly. When a blueberry patch comes into fruit or when a clump of shrubs begins to shed seed, these areas may be visited by mice that would rarely visit them otherwise. The effect of a concentrated food supply in attracting mice is often seen in public campgrounds. Such areas usually have little shelter and much disturbance but abundant food, and sometimes it is possible to trap a dozen or more mice at one spot in a single night. Such numbers are not found under natural conditions. However, Howard (1949) believes that the distribution of food resources has little effect on the movements of *P. maniculatus bairdi*.

An experiment was conducted on Loon's Nest Island to determine whether mice will shift their ranges to take advantage of a concentrated food supply. Previous introduction of mice here had had little success, apparently because emigration was too easy (Sheppe, 1965b). The plan was to put mice and a feeder on the island, determine the ranges of the mice and which mice were using the feeder, then move the feeder and observe any shift in ranges.

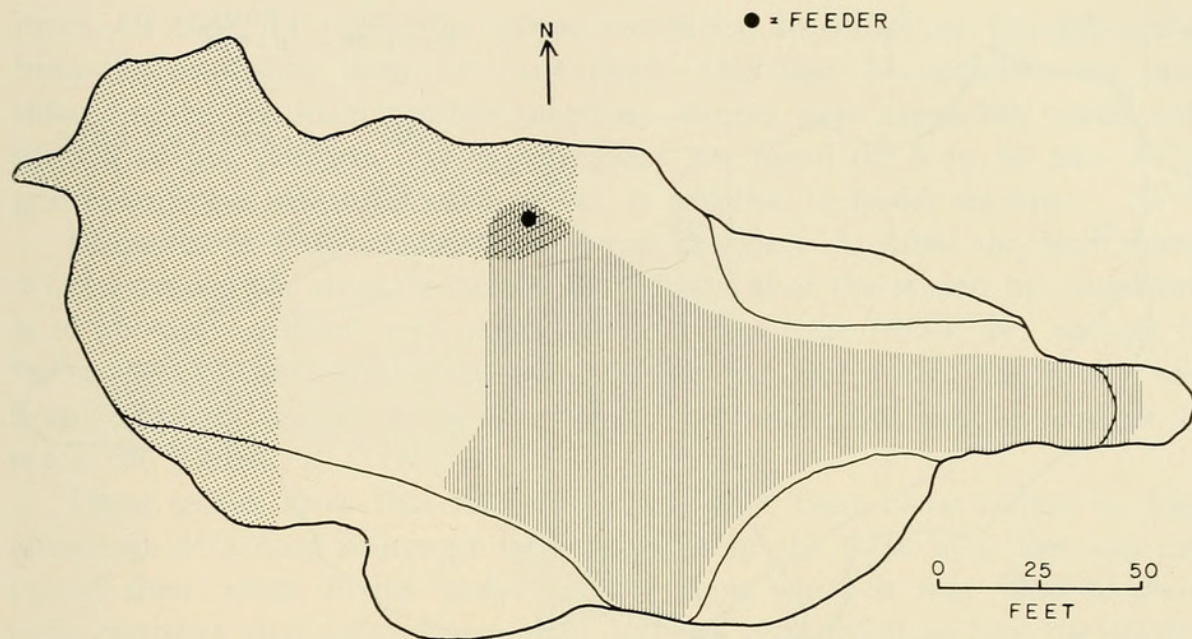


FIGURE 6. Home ranges of the three males that used the feeder when it was in position 1 on Loon's Nest Island. One home range is outlined in ink.

Five male and five female mice were used, of various ages and backgrounds. To prevent the mice from leaving the island before they learned the location of the feeder they were shut in a large pen with the feeder for three nights and then the pen was opened, freeing them to disperse over the island. The feeder was located on the north side of the island near the middle. Within a few nights after the pen was opened the mice had established stable home ranges, as revealed by the grid of tracking stations. Beginning on the fifth night smoked cards were also put in the feeder to determine which mice were using it, but at first these cards were too heavily tracked to give a complete picture of this.

Two of the females disappeared from the island within the first few days. The ranges of the other three were largely separate, but overlapped at the feeder. Three of the males also used the feeder. Two of these had separate ranges, while the range of the third overlapped the others broadly (fig. 6). Each of these six mice was recorded at the feeder 5 to 10 times in 11 nights. The other two males were confined to the south side of the island, but one of them was recorded at the feeder on one night.

After night 15 the feeder was moved to the west end of the island, 105 feet from position 1. Three mice were already using this area, and they used the feeder on its first night in this location. Three other mice used it first on the third night, and one on the eighth. One did not use it at all.

After the feeder had been in this position for 10 nights it was moved 265 feet to the east end of the island. Two mice had been using this area and they used the feeder on the first night, as did another mouse that had not

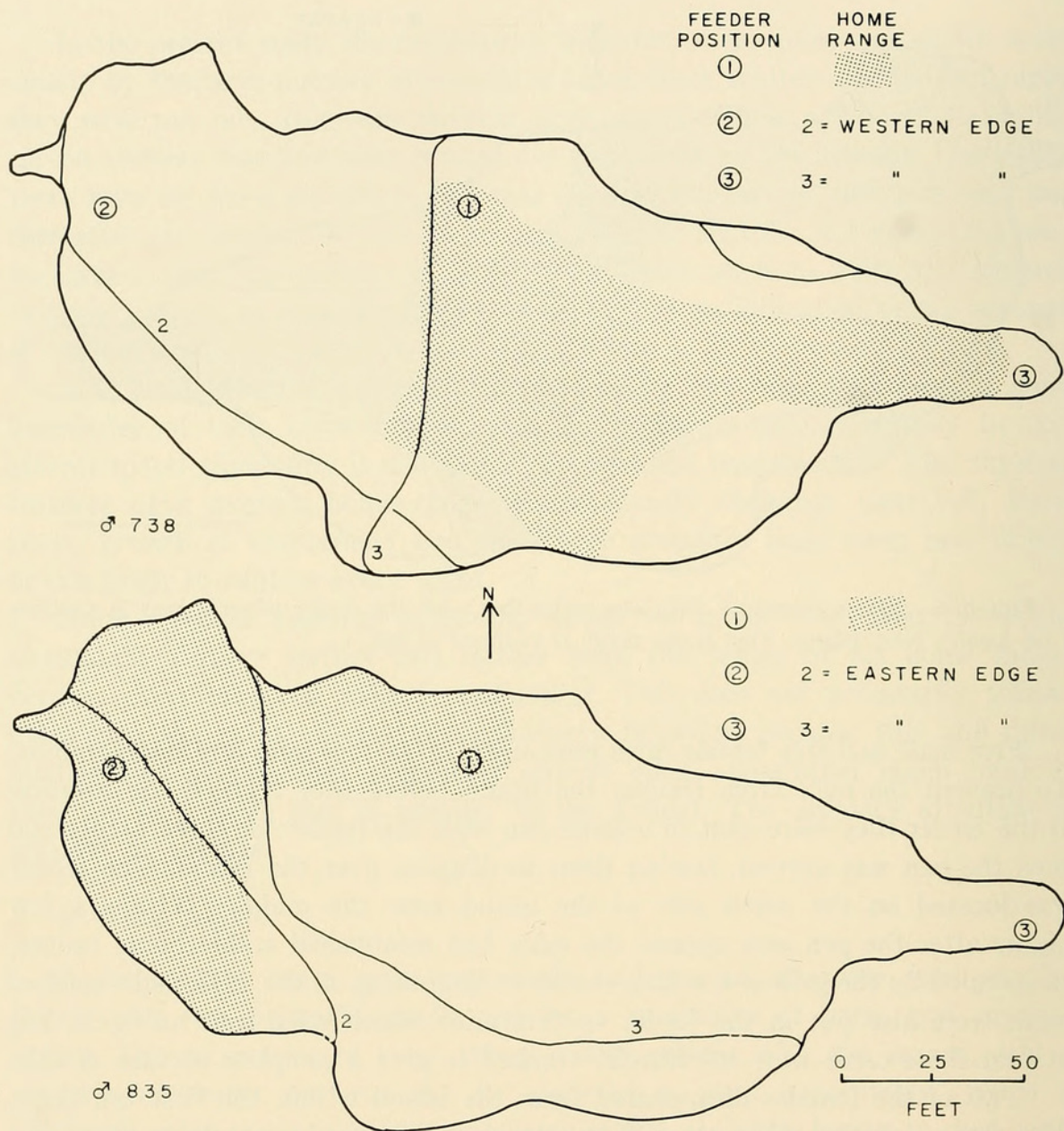


FIGURE 7. Home ranges of two males on Loon's Nest Island when the feeder was in three positions.

previously been recorded within 75 feet of this position. Another mouse began using the feeder on the third night, but two mice did not use it at all. After the 12th night the feeder was removed from the island, but four of the mice that had been using it continued to visit the site for at least a week.

Eight mice were present when the feeder was first moved and six when it was moved again, for a total of 14 moves. The new position of the feeder was within the former range of the mouse five times. Of the other nine times, the mouse extended its range ($\bar{x} = 92$ feet) to include the feeder six times. In other words, the mouse used the feeder 11 times and failed to use it three

times. Of these 11 times, the mouse contracted its range on the side away from the feeder six times ($\bar{x} = 104$ feet). On these 14 occasions the mice showed all of the main possible reactions—ranges were expanded, contracted, shifted, or not changed. The home ranges are based on 4 to 49 ($\bar{x} = 20.3$) grid records per mouse for each period, in addition to feeder records.

Examples of these changes are shown in figure 7. After the first move, ♂ 738 extended his range to include the feeder; after the second he contracted it to about its original area. After the first move the feeder was already in the range of ♂ 835, and he stopped visiting the area where the feeder had been. After the second move he extended his range, but not far enough to reach the feeder.

These results show that mice often will alter their home ranges to take advantage of a good source of food. Presumably the three mice that did not extend their ranges to the feeder did not know where it was. Two of these mice extended their ranges more than 100 feet, but failed to find the feeder. Their failure to explore the entire island probably was a result of social pressure.

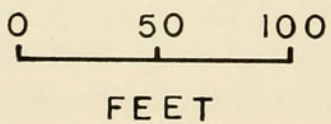
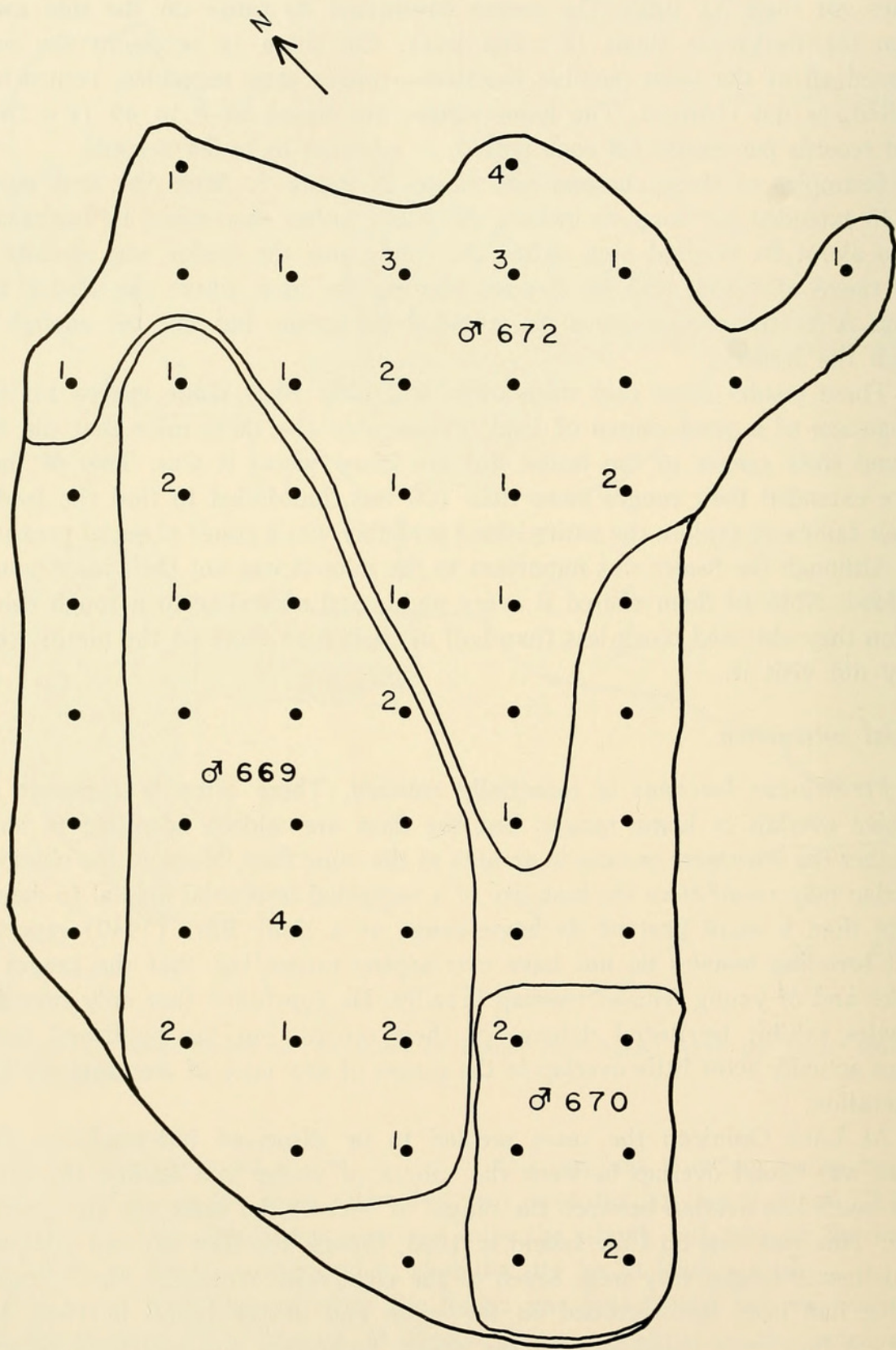
Although the feeder was important to the mice it was not their main source of food. None of them visited it every night, and according to a rough calculation they obtained much less than half of their food there on the nights when they did visit it.

Social interaction.

Peromyscus leucopus is essentially solitary. There often is apparent extensive overlap in home ranges, but the data are seldom adequate to show whether the mice were present in an area at the same time. Much of the observed overlap may result from the inability of a nocturnal terrestrial animal to defend more than a small part of its home range at a time. Burt (1940) reported that breeding females do not have overlapping ranges but that the ranges of males and of young females overlap broadly. He concluded that only breeding females exhibit territorial defense of their ranges, but his published range maps actually show little overlap in the ranges of any mice of the same sex and generation.

At Lake Opinicon the sexes seemed to be dispersed independently and there was broad overlap between the ranges of young and adults, but there was much less overlap between the ranges of mice of the same sex and generation. This was true on Cow Island in 1963, though the data are not adequate to delineate ranges very well. Seven of the eight mice remaining the following spring had been last recorded on the south end of the island in 1963, but in 1964 they were found all over the island, suggesting dispersal from an area of heavy population after the mice on other parts of the island disappeared.

In the small natural population on Sheep Island in early 1964 the three adult males collectively occupied most of the island, but there was virtually no



overlap in their ranges (fig. 8). They were recorded at 27 of the 57 stations on the island, but only one of them was recorded from each of these stations. The ranges of the five adult females overlapped somewhat. These mice had already weaned their spring litters when observations began, and were not pregnant when studied.

These results with natural populations suggest that home ranges are determined in part by social pressure. Experimental evidence for this was obtained by removing individuals and observing the effect on the subsequent movements of the remaining mice. There were five males in the colony on Hump Island in 1963. Male 351 was confined to the south end (fig. 9). Three other males had broadly overlapping ranges over much of the center (fig. 10) and north end, and each of these ranges overlapped the range of ♂ 351 slightly (fig. 11a). These four mice were subadults. The fifth male, an adult, was confined to the north end.

We suspected that ♂ 351 was keeping his three neighbors off the south end, and to test this we removed him from the island. The next night one of the neighbors (♂ 346) moved into ♂ 351's range and thereafter was not found in his own former range (figs. 11a, 11b). The adult male from the north end of the island also began to use the south end on the same night, but continued to use the north end too. The other two males also were recorded nearer the south end than before, but not until several nights later. There seemed to be no effect on the distribution of the five females.

After 18 nights ♂ 351 was returned to the island. For the next 5 nights he was recorded over most of his former range, but the distribution of the other mice remained much as it had been while he was absent. The adult male from the north end left no records during this period, and thereafter was recorded only from the north end. Male 351 disappeared after the 5th night. Apparently he had lost his status while he was away and was not able to reestablish himself when he was returned. His disappearance probably was a result of this.

A similar experiment was performed on Hump in 1964, at a time when one male and four females were present, all of them breeding. The male was using the entire island, ♀ 800 was confined largely to the south end, ♀ 38 to the middle, and ♀ 717 and ♀ 807 had broadly overlapping ranges on the north end. Female 800 was then removed from the island. Female 807 had not been recorded from the south end for 11 nights, but on the night after the removal of ♀ 800 she was recorded almost at the south end. She continued to use the entire island during the 12 nights that ♀ 800 was away and for 3 nights follow-

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FIGURE 8. Records of three males on Sheep Island on nights 1 to 25. Dots show the location of each station; numerals show the number of trap and track records.

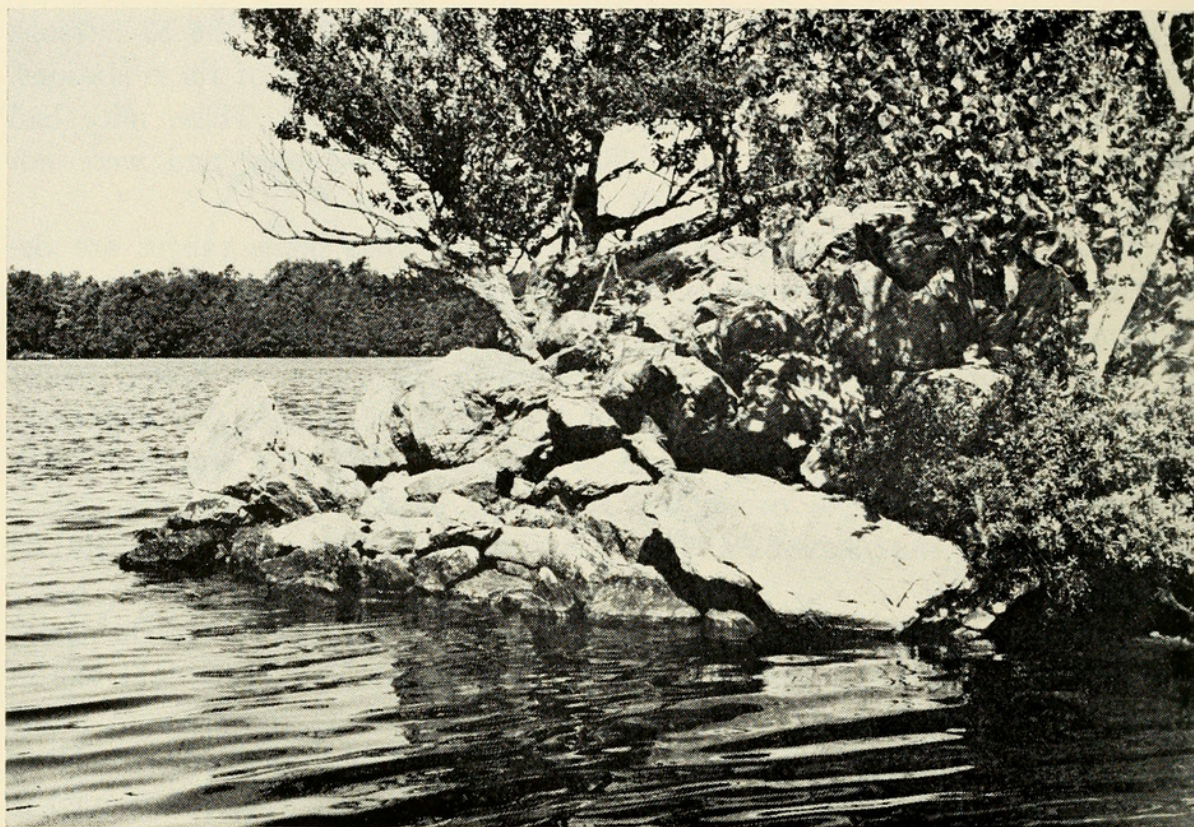


FIGURE 9. The southern tip of Hump Island, showing the broken rock cover.

ing the return of ♀ 800. Thereafter ♀ 807 was confined to the north end again and ♀ 800 to the south end. The ranges of the other two females changed little during this period. Two weeks after ♀ 800 was returned to the island she and ♀ 807 disappeared. Female 38 from the middle of the island immediately extended her range onto the south end and eventually abandoned the middle altogether. Female 717 still was recorded only from the north end.

In the small natural population on Sheep Island in 1964, two adult males occupied adjacent ranges (fig. 8). After ♂ 672 died in a trap ♂ 669 continued to use his own range but extended his movements to include the northwestern part of ♂ 672's range.

Evidence of a slightly different type is provided by a mass removal experiment conducted on Eight Acre Island in 1964. This is the largest island in the lake and in 1964 seemed to have the densest population. A line of 100 traps (line 1) was laid out along the shore opposite Loon's Nest Island to detect movement of mice between the two islands. It was operated at weekly intervals for 9 weeks. After the eighth trapping on line 1, line 2 was set out parallel to it but farther inland. It was operated for 2 nights and then line 3, still farther inland, was set out and operated for 2 nights. The 3 lines were roughly parallel, and all began and ended at the shore. Line 3 extended inland

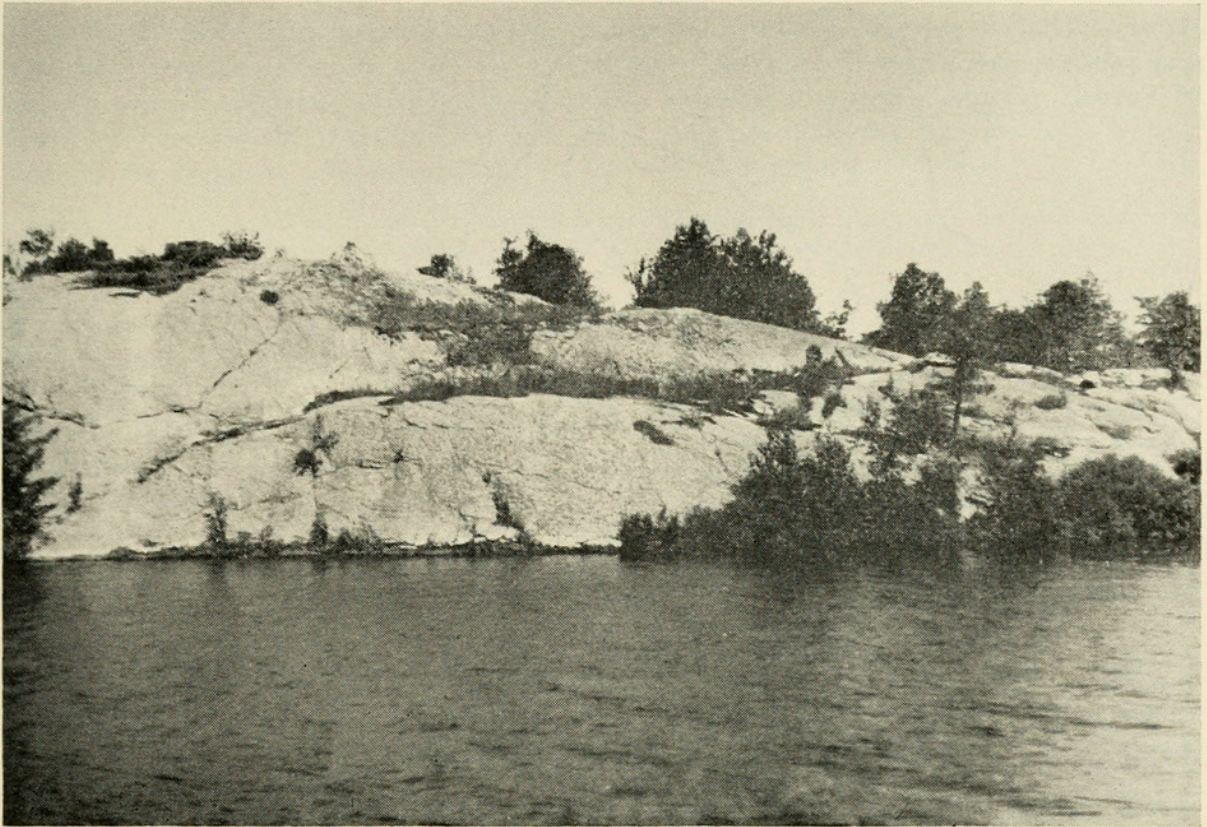


FIGURE 10. The east side of Hump Island, showing the large areas of unbroken rock and sparse vegetation. Male 346 occupied most of this area prior to the removal of ♂ 351.

for about 400 feet at the farthest point. The mice trapped on all lines were marked and released.

After the ninth trapping on line 1 we had a good picture of the population resident along the shore and a partial picture of the population farther inland. On weeks 7 to 9 (a 15-night interval) 16 mice were trapped on line 1. Twelve of these were also trapped on lines 2 and 3. Twelve other mice had been trapped on line 1 on weeks 1 to 6 but not seen anywhere after that. Twenty-four mice were trapped on lines 2 and 3 but not on line 1. Altogether 52 mice had been tagged.

All mice caught on the ninth trapping on line 1 were removed and thereafter line 1 was operated every night for 55 nights and all mice caught were removed. The traps were set again on nights 66 to 68 and all mice caught were released.

The results are shown in figure 12. Twelve of the mice that had recently been trapped on line 1 were removed by the third night, and the remaining four were not seen again. None of the mice from lines 2 and 3 were trapped until night 5, but thereafter these mice were removed at the rate of about one per night through night 22, after which only two were caught. Of the 12 mice that had been trapped on weeks 1 to 5 and not seen since, five were trapped

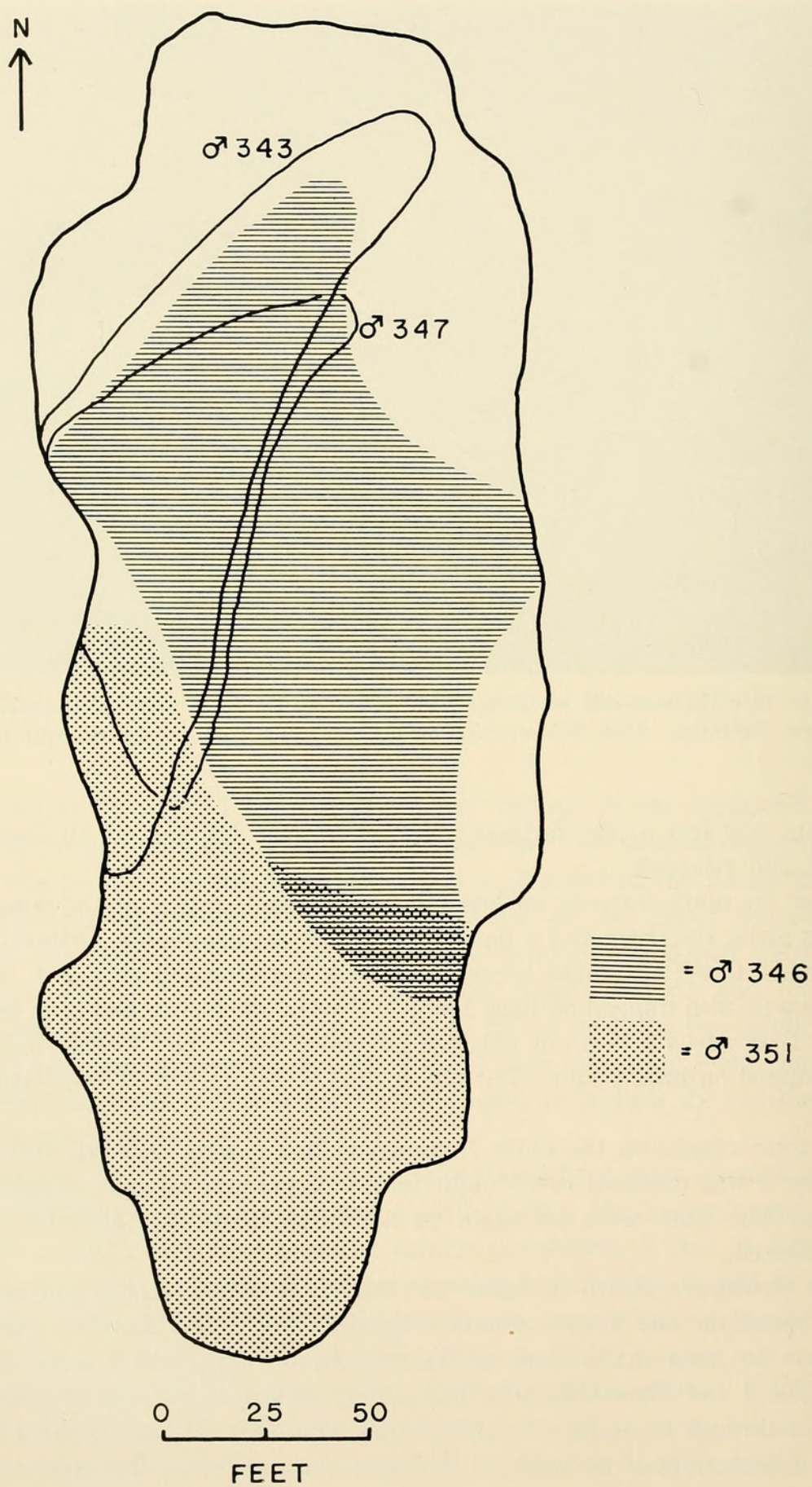


TABLE 2. *Results of removal trapping on Eight Acre Island. Figures for line 1 include only mice trapped there on weeks 7 to 9. Figures for lines 2 and 3 include only mice trapped there immediately prior to the beginning of removal trapping and not trapped on line 1 prior to removal of the resident mice. New mice are those that had not been trapped prior to the beginning of removal.*

	TAGGED ON LINE 1		TAGGED ON LINES 2 AND 3		NEW	
	Young	Adult	Young	Adult	Young	Adult
Trapped and removed	7	5	15	3	46*	5
Not trapped	4	0	3	4	—	—
Percent trapped	64	100	83	43	—	—
Total percent trapped	75		72		—	
Percent young in catch	58		83		90	

* Age of one new mouse was not determined.

again during this period, on nights 3, 16 (2), 17, and 68 (not shown in figure 12).

The rapid removal of the resident mice was not surprising, in view of the ease with which these mice are trapped. Since the mice from lines 2 and 3 were not trapped on line 1 during the first 4 nights it is unlikely that their ranges extended that close to the shore. Their appearance in the traps beginning on night 5 must represent an extension or shift of home range, or at least an exploration out from the range. Presumably few of these changes would have occurred if the residents had not been removed from line 1.

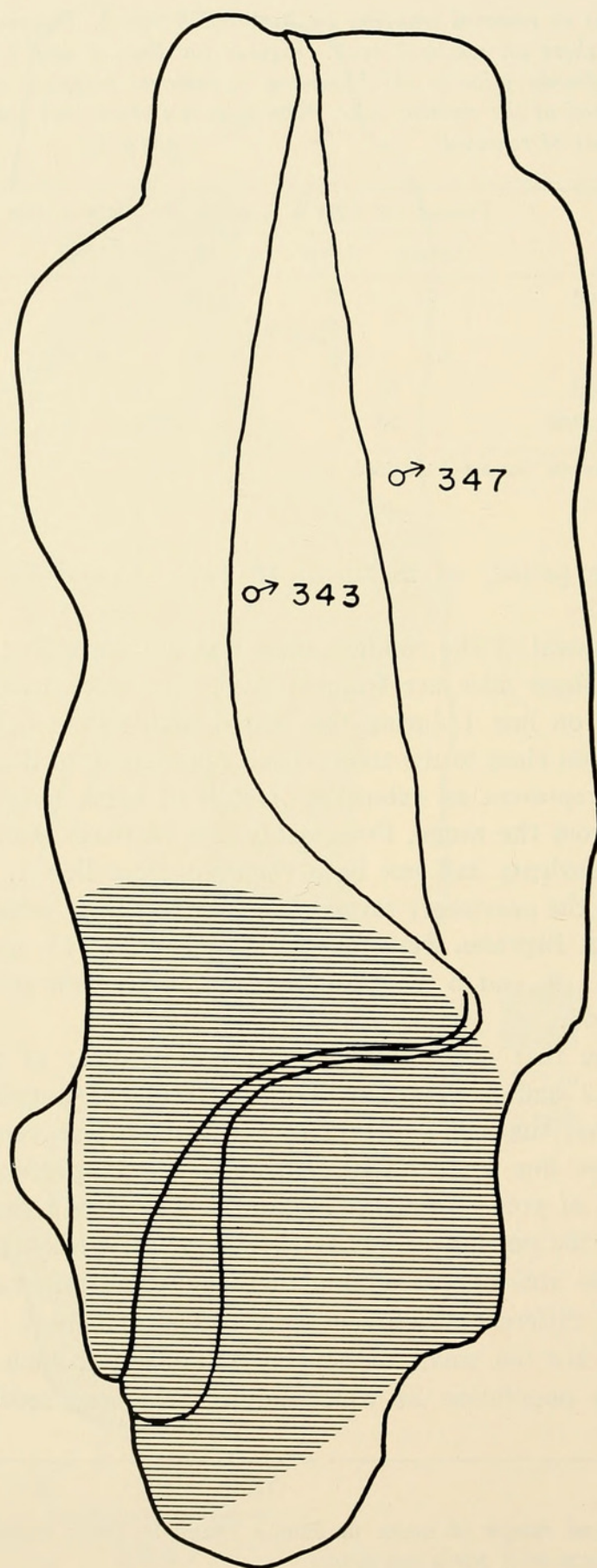
In addition to the previously tagged mice, 43 new mice were trapped during the first 56 nights. Eighteen were caught on nights 2 to 15, and in succeeding 2-week periods 10, 9, and 6 were caught. Nine other new mice were present on nights 66 to 68.

Table 2 shows that approximately the same percent of mice from both line 1 and lines 2 and 3 were caught during removal trapping (75 and 72 percent). However, the age structure of the catches was very different. All of the adults from line 1 were removed, and only 64 percent of the young, while the percent of young from lines 2 and 3 that were removed was almost twice as great as the percent of adults (83 versus 43 percent). The adult invaders entered the area one at a time throughout the removal period. There were no apparent differences between sexes (30 ♂ and 39 ♀ invaders).

The numbers are too small to be very reliable, but such a result would be expected in a population in which adults are more sedentary than the

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FIGURE 11a. Home ranges of males on Hump Island in 1963; nights 25 to 38, ♂ 351 present. The home range of ♂ 354 is not shown.



young. Some of the young mice from line 1 presumably had moved out of the trapping area before removal trapping began and thus could not be caught, while the mice from lines 2 and 3 had to move into the area to reach the traps.

The greater mobility of the young is also shown by the figures on the percent of young in each group. Only 58 percent of the line 1 mice that were removed were young, while 83 percent of the mice from lines 2 and 3 were, and 90 percent of the new mice. Some of the new mice were born after the beginning of the removal period, and if these were excluded the percent of young would be closer to that for lines 2 and 3.

Traps were set on line 3 again on nights 32 to 33 and all mice caught were marked and released. Four mice that had been tagged there a month earlier were still present (three subadults, one adult). One of the subadults was later trapped on line 1. In addition, ten new mice were trapped (seven subadults, three adults). Two of the subadults were later trapped on line 1.

In summary, the resident population had been removed by night 3. Then residents of adjoining areas began to invade the area, and in a period of 18 nights almost all of them entered and were removed. A few of the original residents were still present in the neighboring areas, and other mice had moved in and settled there. There was a small population of mice in these areas that did not enter the removal area even though that area had no residents.

Presumably some of the untagged mice that invaded the removal area were residents of neighboring areas, but a majority of them must have been transients or residents of more remote areas. During the 8-week preliminary period 34 mice were trapped on line 1. Fifteen of these were trapped only once, but the other 19 were known to be present for an average of 4.4 weeks each. During the 8 weeks of removal trapping the line was invaded by 65 mice that were not present there when removal began. This is twice as many as were trapped during the preliminary period. No close comparison of the two periods is possible because trapping effort was much greater during the removal period, but the rate of invasion seems to have been much higher during this period. This presumably was because the residents were no longer present.

Other workers have carried out similar mass removal experiments with small mammals, and usually have found that other animals move in when the original residents are removed. Stickel (1946) plotted the home ranges of *P. leucopus* in a 17-acre area, then removed all mice from the central 1-acre area for 35 nights. The distance from the edge of her removal area to the outer edge of her 17-acre area was similar to the distance between lines 1 and 3 in the present experiment, but there were important differences in shape of area

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FIGURE 11b. Home ranges of males on Hump Island in 1963; nights 39 to 56, ♂ 351 absent.

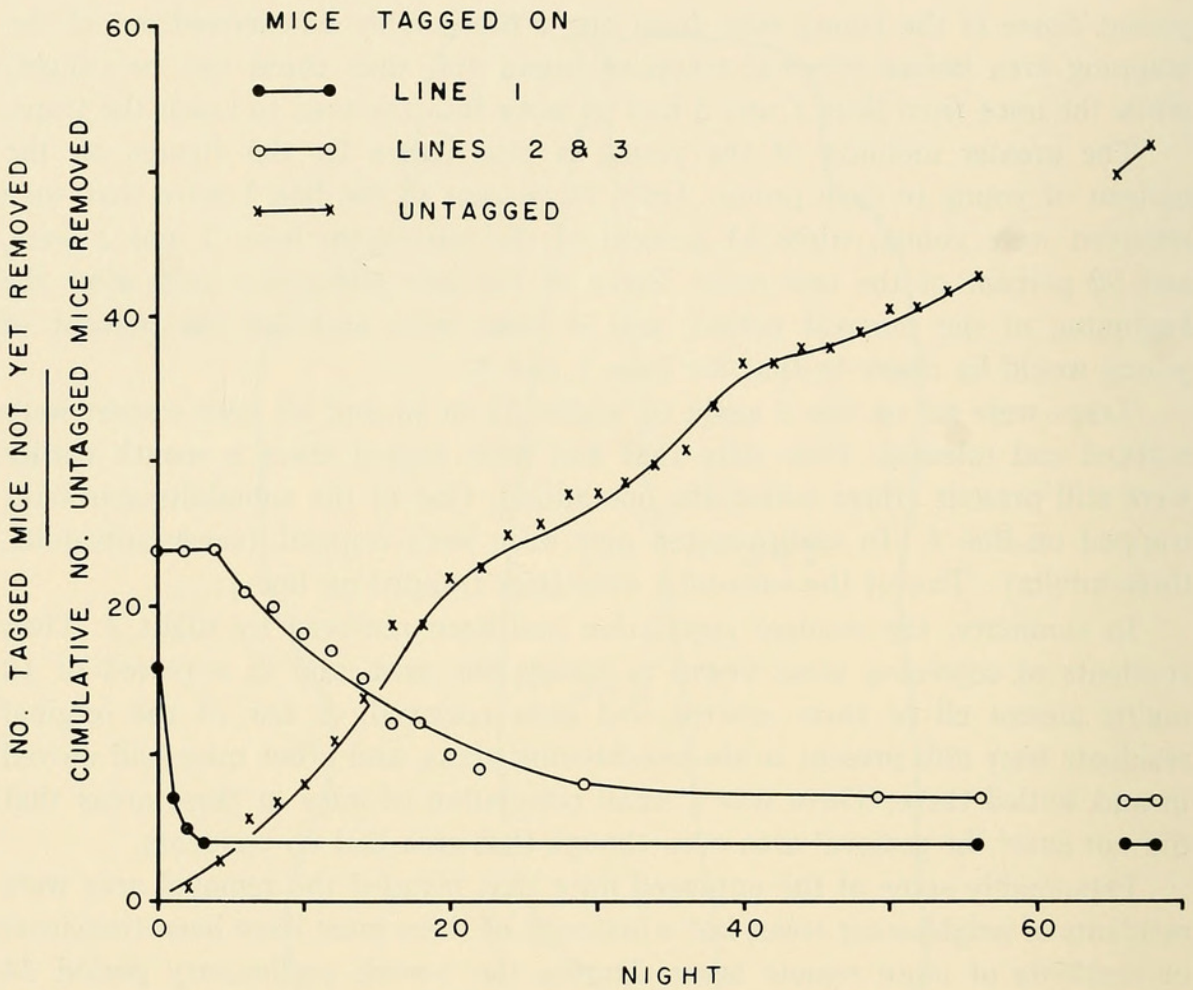


FIGURE 12. Removal of mice from line 1 on Eight Acre Island. Night 1 was July 24-25, 1964.

and in population size. Her adult category presumably consisted largely of mice born earlier in the year, called subadults here.

After 35 nights of trapping she had removed 39 percent of the previously tagged adults and subadults, while in the present study 72 percent had been removed by that time. She did not set traps in her 17-acre area at the end of the removal period to learn whether mice that were unaccounted for were still present. Another striking difference in results is that Stickel found that twice as many males as females invaded the inner area, while on Eight Acre there was a slight excess of females (78 percent of females previously trapped on all three lines were removed in 35 nights, and 71 percent of males).

Most removal experiments have been similar to these in that mice were removed continuously as they moved into the removal area. This makes it impossible to determine the nature of this movement—if left alone would the mouse have returned to its home range and stayed there, would it have abandoned its former range and stayed in the removal area, or would it have

enlarged its range to include both the former range and part of the removal area? The results of removing individual mice, described above, show that lasting changes in home ranges can occur. Blair (1940) removed most of the resident *P. maniculatus bairdi* from a 5-acre plot and within 2 weeks enough mice from outside the plot had moved in and settled there to bring the population up to half its original size. There was little change after this. The source of the invaders is not known, but they presumably came from the adjacent untrapped areas.

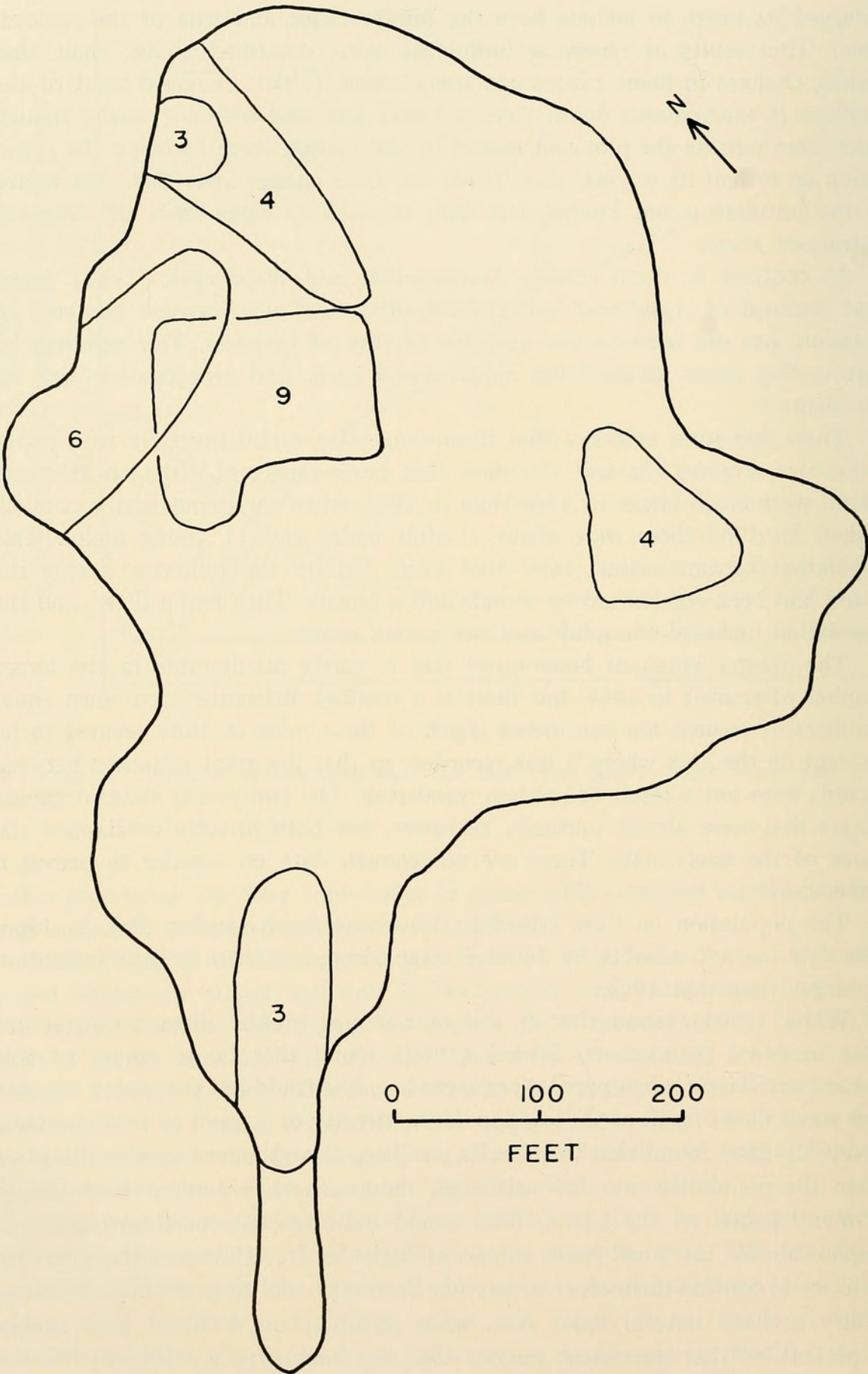
In contrast to these results, Andrzejewski and Wrocławek (1962) found that removal of *Apodemus* and *Clethrionomys* did not increase the rate of invasion, but did increase the duration of stay of invaders. Few residents of surrounding areas invaded the experimental area, and repopulation was by transients.

There was some evidence that home-range size varied inversely with population size. Figures 13a and 13b show that home ranges of males on Hoffman Island were much larger in 1964 than in 1963, when the population was much higher. In 1963 there were about 7 adult males and 11 young males. This population became extinct later that year, but by the following spring the island had been recolonized by a male and a female. They had a litter, and the population included one adult and two young males.

The greater apparent home-range size is partly attributable to the larger number of records in 1964, but there is a marked difference even when equal numbers of records are considered. Each of these mice in 1964 seemed to be resident on the area where it was recorded, so that the great distances between records were not a result of random wandering. The two young males occupied ranges that were almost mutually exclusive, but both broadly overlapped the range of the adult male. There are not enough data on females to permit a comparison.

The population on Cow Island in 1964 was much smaller than in 1963. The data are not suitable for detailed comparison, but there is little indication of larger ranges in 1964.

White (1964) found that *P. leucopus* moved greater distances in sparse than in dense populations. Stickel (1960) found that home ranges of this species were larger when populations were low. She could not determine whether this was a direct result of the low population density or a result of food shortage. Bendell (1959) found that this species on Sheep Island moved greater distances when the population was low, although there was an abundant food supply at many points on the island. This would indicate that social pressure was responsible for the small home ranges at high density. However, the mice are unlikely to confine themselves to any one food type and they continue to range widely and use natural foods even when an abundant artificial food supply is present, so that we cannot assume that any such supply fully satisfies the



needs of the mice. There also were seasonal differences between Bendell's sparse and dense populations. Higuchi (1963) found that *Clethrionomys* had smaller home ranges in large populations than in small ones, which he attributed to territoriality.

The results on Hoffman could be attributed to either food shortage or reduced social pressure in 1964, but there is no reason to believe that there was a food shortage. The Hoffman population had become extinct in 1963 and there should have been an abundant supply of food that had accumulated while the island was uninhabited. The complementary distribution of the two young males suggests that they were avoiding each other, and by extension that the mice in 1963 also restricted their movements in order to avoid other mice.

These results show that social pressure often affects the movements of the mice, but they do not show the nature of this pressure. There could be aggressive interaction between mice, or mutual avoidance with little or no direct contact. There is overlap of home ranges, but this may result from the inability of a mouse to control more than a small part of its range at a time. Two mice may use the same area at different times, and hence rarely meet.

In laboratory pens there is aggressive interaction between *P. leucopus*, especially males, when they first meet (Sheppe, 1966c). When a new mouse is put in a pen where another mouse is living, the resident is intensely aware of the newcomer but does not attack him at first. Eventually the mice make direct contact and there may be a fight, but in some way the resident establishes dominance and begins a long series of brief chases. In these pens there was little fighting and no injury, but there often was persistent chasing. Southwick (1964) has observed frequent killings under similar conditions. The results reported above probably were caused at least in part by such aggressive behavior. A mouse probably does not attack an intruder unless the intruder remains in the resident's area. If there is an attack the intruder will be chased out of the area and the aggressive behavior will quickly stop.

Ordinarily most or all of an area is used by one or more mice, each of which is resident on part of the area. Therefore the relations between any two mice of similar age and sex will be different in different areas. At high population densities even adult males have greatly reduced home ranges, showing that social pressure affects all of the mice, not just a subordinate class. In the laboratory, resident males seemed to be very much afraid of

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FIGURE 13a. Home ranges of males on Hoffman Island during the period June 23 to July 10, 1963. Numbers are the total numbers of trap and track records. The mouse with six records was adult, the others young.

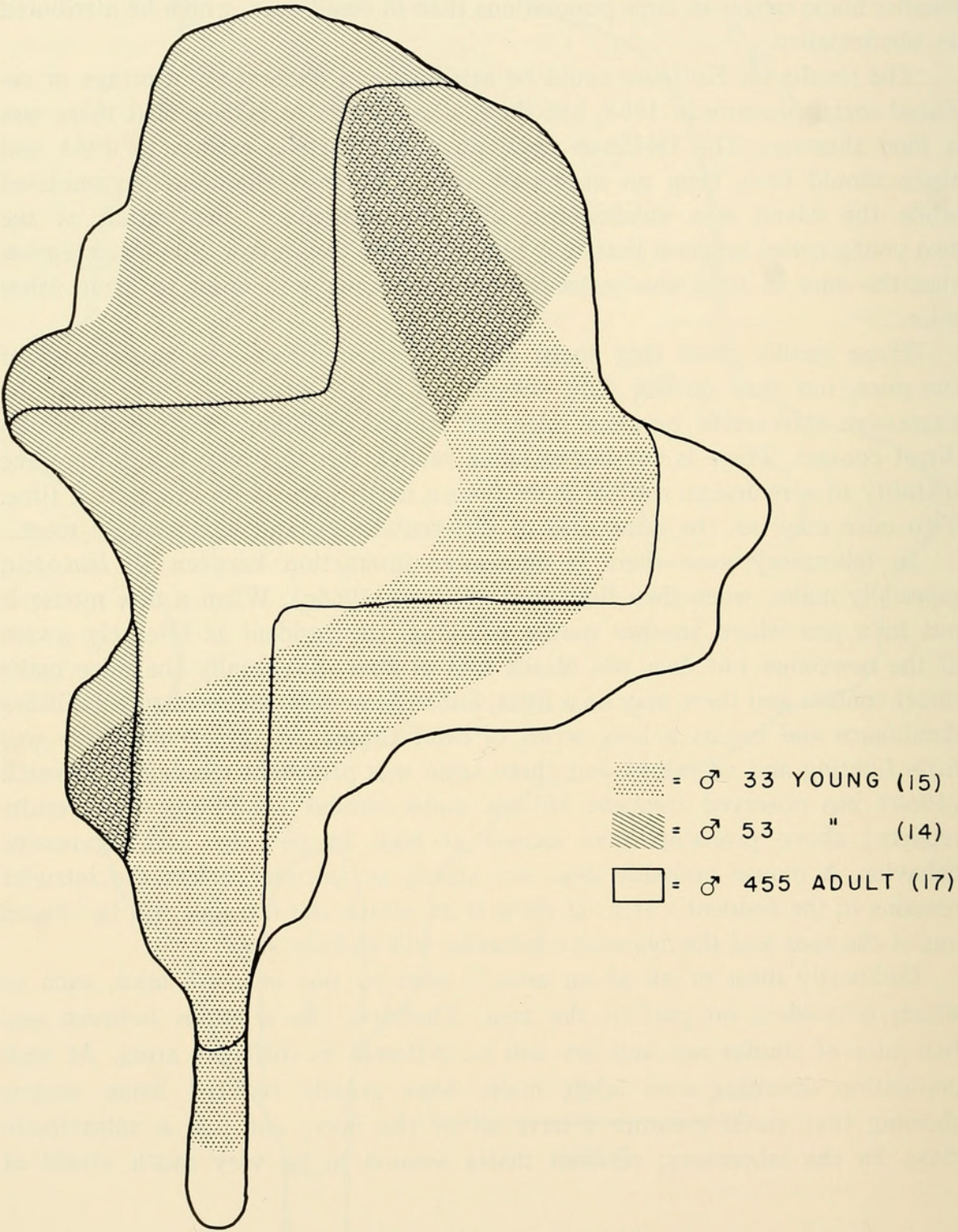


FIGURE 13b. Home ranges of males on Hoffman Island during the period June 23 to July 10, 1964. Number of records is shown in parentheses.

newcomers at first, although they always established dominance over them eventually.

Such social pressure may also occur between different species. This is well known in *Sciurus* and other rodents. In British Columbia, Sheppe (1961) found only *Peromyscus oreas* in a moist ravine and only *P. maniculatus* on the surrounding drier hillsides, with a narrow zone of overlap. When he removed all representatives of *P. oreas* some individuals of *P. maniculatus* then entered the ravine.

Not all social interactions are hostile. Sheppe (1966c) has listed a number of positive interactions observed in laboratory pens. The most common is group nesting. However hostile mice were when active at night, they almost invariably nested together during the day. This is not true in the field, at least during the season when this study was made. Nicholson (1941) found that *P. leucopus* usually nested singly in his artificial nest boxes in summer, but that group nesting was common in winter.

Mating is the most important positive interaction, but there seems to be little if any lasting pair bond. This was true in a few observations in the laboratory, and also in Nicholson's nest box study. Often the mice that were released on the islands in the present study had been caged in bisexual pairs for some time, but the male and female almost always dispersed independently after being released.

Habit.

A home range is more than just the area that a mouse happens to move through. A mouse has a positive relationship to its range, as shown by the frequency with which mice return when removed from their ranges and released far away, even when they have been held in captivity for several months before being released (Griffo, 1961). The mouse knows the physical features of its range, and a mouse's behavior is different when released within its range than when it is released in an unfamiliar area.

This familiarity with the physical features of the home range is shown well by the reaction of mice to strange objects. When novel track shelters were put out, the mice explored them carefully, as indicated by the large number of track records from these shelters (Sheppe, 1966a). This effect wore off quickly. The mice left far more records at such times than they did when they were first put on the islands. Then all stimuli were novel and there was nothing to cause the mice to concentrate their attention on the track shelters. Shillito (1963) has reported a similar difference with *Microtus*.

Being in an unfamiliar place probably is stressful for the mice and they tend to avoid such areas, but this tendency is partly counteracted by their tendency to explore novel stimuli. Mice may leave their established home ranges in response to a gradient in social pressure, or may expand their ranges if

social pressure is reduced, but some mice maintain the same home range even if there are no other mice in the area. A few of the mice on line 3 on Eight Acre Island remained there and were never found on line 1 a few hundred feet away, even when there were no mice on line 1. Presumably some of the mice that did not enter Stickel's (1946) removal area still were present on their original ranges outside, as were most of the resident mice in the study by Andrzejewski and Wrocławek (1962).

A clear example of this was provided by two mice on Hoffman Island in 1963. Originally this island had a dense population and the home ranges of the mice were relatively small. For some reason all of these mice then disappeared, except a subadult male and an adult female. Both of these mice continued to use their original home ranges. They may have enlarged them somewhat, but most of the island was not visited at all by these mice. On the last 16 nights that other mice were present, the male left 9 records at five stations, the greatest distance being 150 feet. On the next 18 nights, when there were no other mice in the area, he left 24 records within the original area and 15 at adjoining stations.

This apparent enlargement of range must have been caused at least in part by the greater number of records, and he was not recorded more than 50 feet from the original range. The greatest distance was 250 feet. Trapping was done again for 2 nights a month later and he was found once within the same range and once 220 feet from the nearest previous record. Six weeks after this traps were set for 2 nights and he was found near the same two places, 360 feet apart.

Apparently this mouse retained essentially his original range for at least 18 nights, but later greatly expanded it. Even then his apparent home range was much smaller than those of the three males present in 1964. He had originally entered a dense population with much social pressure and accordingly established a small home range, while the mice in 1964 had been free to establish large home ranges from the start.

Habit and individual preference affect not only the location of the home range, but also the pattern of use of different parts of the range. The colonies on Hump Island in the 2 years showed similar patterns of preference for some stations and avoidance of others, but there was little correlation between the stations where they were recorded most often in the 2 years ($r = 0.234$, almost significant at the 5 percent level). There seemed to be no habitat differences between the 2 years to account for this. An area may have been occupied by a good tracker in one year and a poor tracker the other, but this was not a major factor. The south tip of the island was a natural unit, isolated by less favorable habitat, and mice that lived there used the entire tip. For the six southernmost stations the ratio of 1963 records to 1964 records ranged from

1:0.4 to 1:5.8, and there was no correlation between the two years ($r = -0.030$). This difference between the 2 years apparently resulted from different habits of the mice that lived there.

DISCUSSION

These results show that the location and use of a home range are influenced by a variety of factors:

1. All parts of the home range must be physically accessible. Sometimes it consists of separate parts connected only by pathways through unsuitable habitat. It may contain areas that are never visited by the mouse.

2. It must be perceptually suitable. When a mouse has a variety of habitats to choose from it will choose the most satisfactory, that is, the one that presents the best combination of perceptual characteristics. This usually will be the habitat where chances of survival are best, but suitable habitats may be avoided because they are perceptually unsuitable (Sheppe, 1965b).

3. There must be sufficient resources of food, water, and shelter.

4. The features of the home range are known to the mouse, having been learned through exploration.

5. All parts are used regularly by the mouse. The meaning of "regularly" must be arbitrary, and some parts will be used more than others.

6. The mouse can maintain itself in the social structure and has a competitive advantage over aliens of the same age and sex. Some type of territorial defense probably occurs.

7. The mouse may have a positive attachment to it that will cause him to return even if released in suitable habitat elsewhere.

The first three of these characteristics apply to any habitat suitable for any animal. It is the last four that distinguish the relationship between a resident mouse and its home range from that between a transient and the area that it wanders through. There presumably is a wide variety of such relationships, involving different combinations and intensities of these characteristics. A mouse may learn the features of an area without being able to establish itself in the social structure. Some parts of the range will be used, known, defended, more than others, but it seems premature to attempt a statistical description of home range until adequate means of observing these things are available.

All of the possible determinants of home range tested in this work were found to influence the movements of the mice at times, but no type of manipulation produced consistent results. Sometimes the removal of other mice or the moving of a food supply seemed to cause remaining mice to alter their home ranges, but at other times habit was stronger and ranges remained unchanged.

Social pressure apparently plays a major role in determining the dispersion of the mice. The nature of this pressure is not known, but it almost surely

varies from mutual avoidance to physical attack on intruders. There probably is little fighting, frequent chasing, and habitual avoidance of contact with other mice. Limited evidence suggests that dispersion is primarily in relation to mice of the same sex and age. Adults presumably have a competitive advantage over the young, but it may be that the young are tolerated more than other adults would be.

Home range is of interest to the extent that it affects more basic aspects of the biology of the species, one of which is population density. Food may be the ultimate factor limiting population size, but populations usually stay well below the limit set by the food supply. Wynne-Edwards (1962) has recently reviewed the evidence that there are mechanisms of self-control that permit populations to regulate their own density to some extent.

Most theories of the self-limitation of population size are based on the supposed effects of social pressure—increased emigration, higher death rate, and lower reproductive rate. The actual role of these effects under field conditions is not well understood, and undoubtedly is highly variable.

The amount of social pressure is determined by the dispersion pattern of the population, and it is here that home range may be involved in the control of population size. If home ranges were mutually exclusive and of fixed size, this would set a maximum density that the population could not exceed. Instead, the home-range size of *P. leucopus* is flexible and there is some overlap of ranges. It is probable that as density increases the first adjustment made by the population is a reduction in home-range size. Home ranges are not infinitely compressible and as density increases still more they will approach a minimum size (Southern, 1954, for *Mus*) and the population will adjust by an increasing amount of overlap of home ranges. Both of these adjustments will increase social pressures, which could be expected to have the results listed above.

The behavior of the populations at Lake Opinicon did not conform very well to this theory. The most important mechanism of self-limitation of population size seemed to be the low reproductive rate. Most females had a litter in the spring and perhaps another in late summer, but there was little breeding from mid-June to mid-August. This was true over a wide range of population densities.

On the other hand, mice introduced to previously uninhabited islands during this season often began to breed soon after release, although these populations were at much higher density than any natural population (Sheppe, 1965d). Because of this unseasonal breeding some populations grew rapidly within the first few weeks after being established. This breeding did not seem to be a result of better nutrition. It probably was a part of the behavioral disruption caused by the unfamiliar situation, including perhaps both the physical and the social environments.

This suggests that home-range contributes to the stability of *Peromyscus* populations by enabling each individual to live in a relatively stable environment. This stability promotes individual survival and also facilitates maintaining a breeding rate that has been determined by natural selection. Breeding may be limited by a psychological-physiological condition associated with stability of social and other stimuli, even when other conditions are favorable. When this stability is destroyed, breeding may begin at a time when it would not otherwise occur.

In the present work this unseasonal breeding probably was maladaptive because it produced densities that would soon have destroyed the food supply, but under natural conditions of colonization such breeding might be advantageous. Natural colonies usually are established by a very small number of immigrants. If an area is colonized by a single male and female, one of them might die or leave before the next regular breeding season, but if they breed at once the population can quickly be built up to a safer size. It may be that similar unseasonal breeding occurs when a population is greatly reduced by some catastrophe (Davis and Christian, 1958). Both the limitations on breeding in natural populations and the removal of these limitations under certain conditions may promote survival of the population and hence may be a result of natural selection.

We can speculate that the unseasonal breeding of the Lake Opinicon colonies was an accidental result of a species characteristic that evolved in response to similar but not identical conditions. Perhaps the novelty of physical and social stimuli is the proximal mechanism that triggers breeding under such conditions, and the rapid build-up of the population is the ultimate function of this breeding. In the artificial colonies population density was already high, but the proximal stimuli to breeding were present and the mice responded accordingly.

Most of our knowledge of small mammal populations has been gained from descriptive studies of natural populations or experimental studies of laboratory populations. Both of these approaches are of value, in fact the former is essential, but both have serious drawbacks. Descriptive studies usually provide little information on the causes of the observed phenomena, and laboratory studies must be carried out under conditions so artificial that the results may be misleading if extrapolated to field conditions.

A number of workers have used a third approach, the field experiment, and the principal purpose of the present work was to apply this approach to help clarify the relation between small mammals and their environment. Field experiments permit the manipulation of environmental and population factors to test the effect of each, yet they are conducted with populations under natural or seminatural conditions.

The field experiment is a powerful tool and has already cast much light

on small mammal population problems, yet it has serious drawbacks that must be understood in conducting the experiment and interpreting the results. In the present study neither controls nor replications were possible. There were 57 islands in the lake, but no two of them were sufficiently alike in area and habitats to be paired for experimental purposes. The same experiment could not be conducted twice in succession on one island, because no two seasons or years are sufficiently alike, and each replication alters the conditions on the island. There is great variability among the mice, yet if individual mice are to be studied in detail presently available techniques can be used only with small populations.

Not only was it impossible to provide suitable controls and replications, it was not even possible to plan the details of any experiment in advance. Habitat conditions, population size and structure, and the behavior of individual mice could not be predicted. Work with each population was begun with one or more experiments in mind, but it was always necessary to alter the details to suit conditions that developed, and sometimes an experiment had to be abandoned when a population became extinct or a key mouse disappeared.

Because of these difficulties it may never be possible to carry out a carefully planned and controlled series of experiments designed to clarify a particular problem. It is desirable to accept this limitation and work within it, rather than attempt to carry out a predetermined experimental program under conditions that are not suitable. Such work will be opportunistic, and the results usually will be suggestive rather than definitive. Confidence in interpretation will come with the gradual accumulation of experimental results related to each problem. These results probably will accumulate slowly, because each experiment requires far more work than a comparable experiment in the laboratory, some experiments will produce no results at all, and no two experiments will be fully comparable.

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