SOCIAL FACTORS INFLUENCING SPATIAL DISTRIBUTION IN POPULATIONS OF PRAIRIE DEERMICE

By

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AN ABSTRACT

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ABSTRACT

Factors influencing the geographical distribution of a species are effective through the local population. Therefore, the study of spatial distribution within local populations offers a "dynamic" approach to problems associated with the spread of a species over its broad geographical range.

This study combined laboratory and field techniques in order to examine the importance of social factors to the spatial distribution of local populations of Prairie Deermice (Peromyscus maniculatus bairdii).

The objectives were:

1. To study the effect of social manipulation of deermice populations in the laboratory upon their subsequent spatial distribution in a semi-natural environment.
2. To examine behavioral patterns effecting spatial distribution in free ranging, semi-natural populations.
3. To measure the individual awareness of, and preference for, the home area as well as the stability of such an area.

Successive populations of deermice were raised from weaning age (21 days) in isolation or in groups. At ten weeks of age, four bisexual pairs from each social treatment were systematically released into different one-half

acre "mouse-proof" plots. There were 8 experimental periods between June 6 and November 21, 1958, during which 8 successive populations of four bisexual pairs were living in each of the two plots.

Following release into the plots, the daily occurrence of the mice in nest boxes was recorded. Seventeen days after release, all mice were taken to the laboratory for 36 hours. Each was then reintroduced into its home plot at a point distant to its previously established home area. The location of each mouse for the next three days was recorded. In the last 3 experiments, young alien mice were retained in one-half the nest boxes during the first night after reintroduction of the residents. At the conclusion of each three week experimental period, all field experimentals and their laboratory controls were killed, weighed, and the adrenals removed and also weighed.

Other dynamics of the populations were measured by two periods of live trapping, by recording the time and frequency of feeding activity, and by direct observation of social interaction between residents and aliens.

The "mouse-proof" field proved to be an effective method for the study of population dynamics under semi-natural conditions while maintaining a measure of the controlled conditions which are possible in the laboratory.

Phenomena which may be specific to populations of prairie deermice, to mice of the species _Peromyscus maniculatus_; or which may have general significance to small mammal populations were suggested by this study.

a. Between 55 and 60 per cent of the mice moved to different nest boxes each night. Less than half of these moves were to boxes previously unvisited by the mouse moving. These data indicate that each mouse maintained several refuges and/or nest sites rather than a single one around which its activity centered.

b. During the breeding season, the prairie deermice in this study were generally found alone or in bisexual pairs and rarely occurred in a nest box with an animal of the same sex.

c. Mice of the opposite sex succeeded each other in nest boxes on successive days significantly more often than those of the same sex. Females followed males into boxes significantly more often and males followed females significantly less often than expected by chance.

d. No reliable evidence for territoriality was obtained. The data indicated that animals of the same sex were spatially segregated as a result of a negative repulsive force, hypothetically, avoidance.

e. Mice of both social treatments homed significantly more often than expected by chance. Such performance indicated that the individual mice recognized both their "own" nest boxes and those of their neighbors. Thus, a spatial distribution framework or "positional stability" may be a characteristic of local populations.

f. Mice of both social treatments homed significantly less often to nest boxes temporarily occupied by young aliens than they did in the experiments prior to the introduction of aliens. This decrease in homing supports the hypothesis that the spatial distribution of prairie deermice may be achieved through mutual avoidance of individuals. Extension of the range of the local population as well as of the geographical distribution of the species may be largely by a diffusion-like process. Young mice, upon leaving the home nest site may move into an occupied area or into a temporarily empty nest site rather than moving long distances until an unoccupied area is found. Such behavior could cause a partial displacement of the residents due to avoidance and result in a gradual extension of the range at the periphery.

The differential effects of the social treatments were as follows:

a. The isolation raised mice combined with others less often than the group raised mice; were slower in combining; and generally maintained a greater distance from their fellows.

b. The isolation raised mice homed significantly more often than group raised during the experiments when homing was established as a phenomenon. The introduction of aliens into one-half the nest boxes had a more adverse affect upon the homing performance of isolation raised mice than of group raised.

c. The isolation raised mice appeared to be less sociable and more spatially oriented than group raised.

d. The data suggest that spatial patterns of distribution existent in the plots were largely determined by social interaction and were of greater significance to isolation raised mice than to group raised. Isolation raised mice adapted less easily to changes in the social and related spatial stimuli than the more sociable group raised mice and, thus, more frequently returned to the earlier established spatial patterns. The introduction of aliens disrupted the social-spatial equilibrium existent in the plots. This disruption had a more severe and longer lasting affect upon isolation raised mice than upon group raised due to the inability of the former to quickly adapt to the environmental changes.

e. Differences in social behavior have been shown to be important factors determining spatial patterns of distribution within local populations. The importance of social factors to the evolution, genetics, and dynamics of populations is, therefore, evident.

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INTRODUCTION

The distribution of an animal species in space may be geographical or local in scope. Geographical distribution of a species is measured in terms of the range of occurrence of its naturally existing populations. This treatment of distribution is essentially historical and has great descriptive and comparative value. A species, however, is a "dynamic system" (Blair, 1956), whose basic components are local populations (Mayr, 1942) existing in equilibrium with the ever-changing environment. Therefore, the study of factors influencing spatial distribution within local populations offers a "dynamic" approach to many problems associated with the spread of a species over its broad geographical range.

The Biological Importance of Spatial Patterns to Populations

Species evolution. Local populations must not only be considered as important effectors of the distribution of a species, but they are also the operational units of evolution. The relationship of spatial distribution within local populations to the evolution of the species is a complex one. The amount of inbreeding and the rate of spread of genetic factors are functions of the mobility and dispersal tendencies of individuals of the population. The mobility and dispersal of individuals may be influenced by physical factors of the environment such as food, nest sites, barriers, etc., and by sociobiological factors such as territoriality, dominance-subordination, dominance-submission, intra-specific social tolerance, and assortative mating. The spatial patterns of distribution within local populations reflect, partially at least, those forces affecting the evolution of a population.

Population control. Populations characteristically grow in a manner described by the logistic curve (Allee, et al, 1949, p. 304; Andrewartha and Birch, 1954, p. 348). That the logistic curve of population growth merely fits the data and cannot be considered a law of population growth for extrapolation and prediction, has been pointed out by numerous workers, e.g., Cole, 1957; Southwick, 1956; Wilson and Puffer, 1933. It follows, therefore, that the artificially derived constants of this curve should not be interpreted as the constants of nature with relation to population biology (Allee et al, 1949, p. 304). As a population approaches the upper asymptote of the logistic curve permitted by the environmental conditions, growth is arrested by a reduction in the contribution of progeny to the population. With the passage of time, populations tend to remain at equilibrium with the environment. This equilibrium has been defined as "the average size held by a population over a considerable period of time" (Allee, 1949, p. 315) and as such exhibits a range of variability.

In general, factors controlling animal populations have been divided into two groups: those that are dependent upon population density and those that are independent of population density (Dice, 1952, p.344; Smith, 1935). Density-dependent controlling agencies are mostly biotic in nature and are believed to be the ones that principally determine the equilibrium density of populations. Density-independent agencies are mostly climatic.

It should not be thought that the above two groups of factors affecting populations are mutually exclusive. Nicholson (1957) states that the same factor may be density-dependent in one situation and density-independent in another. Much of the confusion surrounding these two classifications of factors is due to the ambiguous use of the term "density-dependent factor" as originally defined by Smith (1935). He used the term to designate factors which were so influenced by population density that they opposed with greater intensity at higher densities than at lower ones the innate tendency of populations to grow.

Most prominent theories of the control of natural populations vary in the degree of importance assigned to the density-dependent factor of intraspecific competition. Andrewartha and Birch (1954) stressed a comprehensive approach in which all types of factors are involved in population control. In Milne's words (1957) this theory may be summarized as follows:

> "Natural control is a matter of numbers increasing and decreasing just so long as the environment permits; environmental conditions fluctuate and the requisite conditions do not endure long enough either for unlimited increase or for decrease to zero; the ruling components of environment in this respect are multifarious and by no means confined to competition (intraspecific or interspecific), parasites, predators and pathogen."

Another widely accepted theory of population control stipulates that the only factors able to control are those whose actions increase in severity as density rises (Cole, 1957; Lack, 1954a, 1954b; Nicholson, 1933, 1954a, 1954b, 1957; Nicholson and Bailey, 1935; Smith, 1935). Milne (1957) in his recent review outlined this theory as having the following two tenets:

> "1. That the environment is comprised of density-dependent and density-independent factors;
> 2. that (a) controlling factors must be density-dependent, and (b) the chief of these are (i) competition within the population itself and (ii) the affect of enemies."

Lack (1954a, 1954b) emphasized the importance of food shortage, predation, and disease as factors causing higher death rates at higher population densities. Nicholson (1954a, 1954b, 1957) goes further by postulating (1954b) that "the mechanism of density governance is almost always intraspecific competition, either amongst the animals for a critically important requisite, or amongst natural enemies for which the animals concerned are requisites".

Most theories of population control (of which the above are examples differing widely in their emphasis) suggest that intraspecific competition, while differentially evaluated as to its importance, may be effective in controlling populations.

Requisites promoting intraspecific competition among the individuals of a population include food, water, nest sites and any protected associated area, mates, and other non-sexual social relationships (Scott, 1956). Competition for these requisites is not only a function of the number of animals present but is also determined by what Frank (1954, 1957) termed the "Condensation Potential" of the species.

The condensation potential consists of behavioral mechanisms that enable many "cyclic" species to live at an uncommonly high population density. "It is based on all intraspecific and especially social behavior that favors the increase of density" (Frank, 1957). Frank (ibid) further postulated that "the condensation potential is normally limited by intrinsic behavior, especially by territoriality, to a saturation point which is approximately adapted to the carrying capacity of the environment". Davis (1958) refers to the same relationship in a reverse way as the "individual distance tolerance limit" which is a species characteristic and may be so low that individuals can never associate together. This is apparently the "individual distance" concept explored by Marler (1956).

It should be noted that the expression of condensation potential is most noteworthy during the breeding season. This is true because many species aggregate during the winter, supposedly as a heat conservation measure, and then segregate during the breeding season (Howard, 1949; Nicholson, 1941).

The concept of the condensation potential is also applicable to species which do not show the great fluctuations in numbers characteristic of "cyclic" forms. Further, it is indicative of the interaction between individuals of a population related to the area they occupy. As such, the condensation potential is a measure of the relationship between behavior and spatial patterns of distribution.

Calhoun (1952) suggested a behavior - space relationship following an experiment in which a colony of free-ranging rats (Rattus norvegicus) did not increase to over 200 animals while living in the same amount of space in which 50,000 individually caged rats could have been maintained. He concluded that under free-ranging conditions, the rats expressed behavioral potentialities which were impossible in the caged conditions.

Recent studies of laboratory populations in which the physical environment was controlled have shown wide variations in the asymptotic level for several populations in the same amount of space. Table I is a tabulation of several studies showing the range in maximum numbers in the several experimental populations of each study. The data in the table cannot be compared between studies because methods of considering young as members of the total population varied. Also, the environmental conditions under which each study was carried out were different. The variations in maximum population size among the several experimental populations of each study appear to be due only to behavioral differences in the social structure of each population.

TABLE I

VARIABILITY OF POPULATION ASYMPTOTIC LEVELS WITHIN EXPERIMENTS

Study	Animal	Enclosure Size	Number of Enclosures	Number of Animals at Asymptote
Brown (1953)	<u>Mus</u> <u>musculus</u>	6' x 4'	4	3 - 19
Christian (1956)	" "	(29" x 74") x 2 decks	4	21 - 120
Crowcroft & Rowe (1957)	" "	6' x 6'	4	150
Southwick (1955)	" "	6' x 25'	6	25 - 120
Strecker & Emlen (1953)	" "	500 sq. ft.	2	48 - 115 (approx.)
Clarke (1955)	<u>Microtus agrestis</u>	"large open-air cages"	2	41 - 58
Louch (1956)	<u>Microtus pennsylvanicus</u>	6' x 25'	3	28 - 67

Evidence contrary to the above was provided by Crowcroft and Rowe (1957) studying four freely growing populations of <u>Mus</u> <u>musculus</u> in pens 6' x 6'. They found a marked difference in the rate of growth of their populations but <u>all</u> contained comparable total numbers after eighteen months One of the populations reached the amazing total of 150 animals or 4.1 mice per square foot!

The previously mentioned wide range of population size between several populations maintained under identical environmental conditions indicates that population density must be defined in terms of units of social pressure which are at present poorly known. Christian (1957) while discussing this concept suggested that the "social structure of a population in terms of aggressiveness of the individual members, their equality or lack of equality and other less well known behavior factors would determine the maximum population density...". Thus, in different populations varying numbers of animals may comprise each unit of social pressure as a result of individual differences in behavior (Brown, 1953; Southwick, 1955; Christian, 1957). The total units of social pressure for asymptotic populations under identical environmental conditions would be the same although the numbers of animals in each population might differ markedly (Table I).

Southwick (1955b), working with laboratory populations of *Mus musculus*, found that fighting varied between populations irrespective of the numbers of animals present in the same size area. Population growth ceased or was greatly impaired through excessive litter mortality when his populations built up to a point at which fighting occurred at the rate of one aggressive encounter per hour per mouse. This point was independent of density within the limits set by the physical environments of the experiments. Christian (1955a, 1955b, 1956, 1957) studying the effects of increase in population density upon adrenal size, reproductive function, and litter survival in house mice found that the physiological alterations were quantitively and qualitatively similar for asymptotic populations irrespective of the actual numbers of animals present.

With the above facts in mind, the question may now be asked how units of social pressure, condensation potential, and population density relate to spatial distribution. How does spatial distribution relate to each of the others? Figure 1 shows the hypothetical interrelationship of these factors. The interactions are complex. They are influenced, and may be controlled by, the omnipresent environment composed of density independent factors and such density dependent ones as disease, predation, and parasitism.

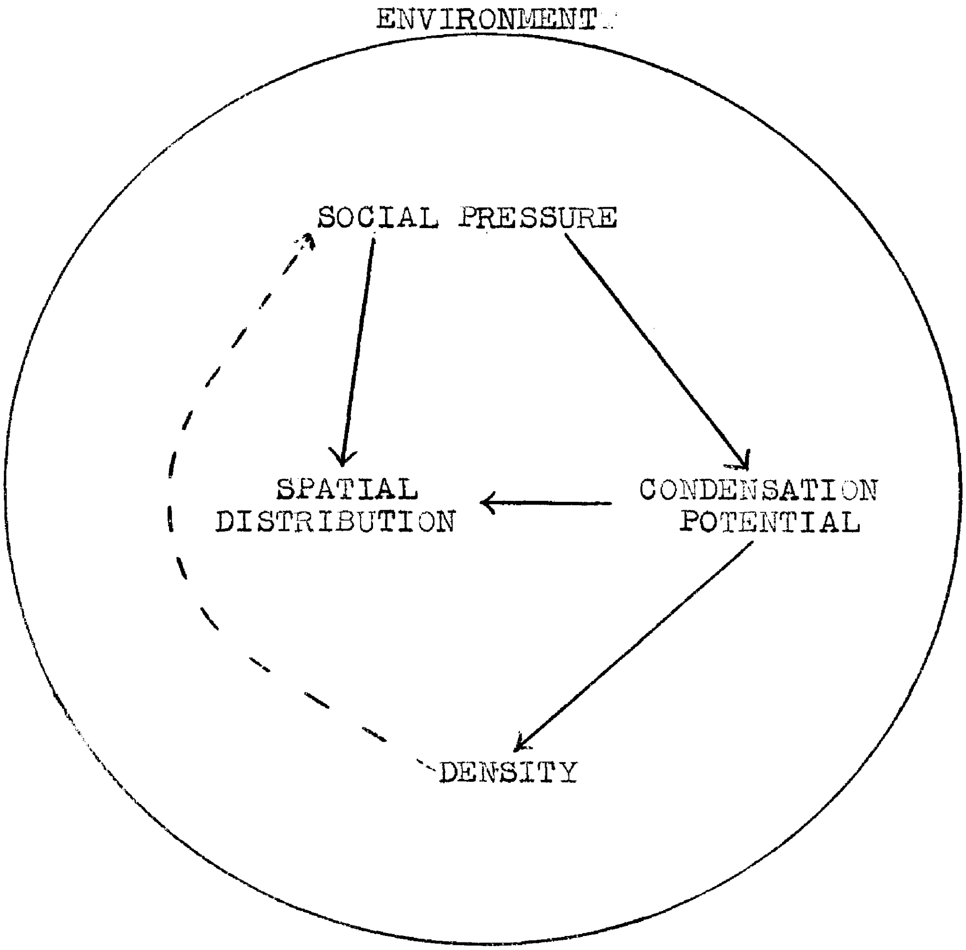

Fig. 1. Interaction of factors affecting distribution within local populations.

Within the environmental complex, social pressure may be the fundamental factor influencing population growth (Christian, 1957; Frank, 1957). It is an intrinsic attribute of each local population and is the sum of the individual differences in social behavior which affect population growth (Scott, 1956). Social pressure effects population control chiefly through increased stress, fighting, and mortality, and through decreased reproduction, maternal care, and survival of young (Brown, 1953; Clarke, 1955; Christian, 1957; Southwick, 1955a, 1955b). Social pressure units are independent of density within limits and are basically ininvolved in the condensation potential of species populations.

For each species population, the condensation potential, as Frank (1957) defined it, has a characteristic value which is related to the carrying capacity of the environment. It is related to distribution in space as well as to the individual behavioral potentialities of the members of the population. Social pressures operate within and upon the condensation potential. Indeed, in experimental laboratory populations, social pressures have been shown to control population growth irrespective of the number of animals living in the available space (Brown, 1953; Southwick, 1955b).

Both the condensation potential and social pressure are effective in determining the spatial distribution of the population. The most important known social factor operating as a component of the condensation potential to control spatial distribution is territoriality.

Density is a term of descriptive value in a broad ecological sense but of questionable value in the study of spatial distribution within local populations and of the biological importance of such distributions. Density is defined as "the number of organisms per unit of space" (Allee, et al, 1949, p. 266) and is found by the following formula:

$$\text{Density} = \left(\frac{\text{Absolute numbers of organisms in area}}{\text{Number of spatial units in that area}}\right).$$

Nicholson (1957) and Cole (1957) suggested that in order to be useful in the study of population dynamics, the above definition of density must be expanded and an implication drawn from it specifically for population application. Cole (1957) stated that density "in this sense, (the population sense) is not the number of organisms per unit area or volume but is the difference between this actual density and that which would prevail at carrying capacity. The concept includes both the effects of crowding as a governing factor...and the effects of environmental inadequacies". Thus, density may mean at least two different things.

The relationship of density as defined by Allee to spatial distribution is also not clear. Density, by definition, is independent of spatial distribution. However, in the broad sense, the pattern of spatial distribution determines the number of organisms in the area. At a constant density, the distribution of individuals may vary from extreme clumping to the maximum equal distribution possible in the unit of area defined by the density measurement. Spatial distribution is dependent upon density since an increase or decrease in the latter will affect spatial distribution when the denominator of the above equation is unity. Such changes in density may not, however, affect spatial patterns in the density defined area when the number of spatial units of the denominator is more than one. Since density used in the descriptive sense obliterates the biologically important concepts of spatial distribution within local populations, a description of animal association and abundance relative to distances separating individuals would appear to offer the best method of measuring these social-spatial-biological aspects of population dynamics.

Within any confined area, density of animals is controlled by social pressures acting through and upon the condensation potential. The experiments of Southwick (1955); Christian (1957) and Brown (1953) suggest that there is no direct relationship between density and social pressure since their populations stopped growing at widely different densities while at similar social pressures.

Factors Affecting Spatial Distribution

Spatial distribution of populations of small mammals living under natural or semi-natural conditions is related in a complex way to the influence of the physical as well as of the biotic environment. The importance of characteristics of the habitat in determining spatial distribution has been indicated by numerous studies.

Brand (1955) studying the White-footed Mouse (Peromyscus leucopus noveboracensis) has shown a direct seasonal relationship between the spatial distribution of the population and tree density, degree of slope, and density of fallen trees. The significant factors of the habitat in this relationship were probably occurrence of food and potential nest sites. Orgain and Schein (1953) effected a decrease in numbers of rats in city blocks for a short period of time by removing harborage sites which existed in excess of need. Davis (1958) changed the spatial distribution within laboratory populations of house mice through introduction of baffles and additional nest sites to the study area. Blair (1951) and Provost (1940) showed the relationship of distribution and abundance to habitat differences.

The location of food as a factor influencing spatial distribution was demonstrated by Calhoun (1949, 1950) with populations of rats (Rattus norvegicus) and by Strecker (1954) with house mice under semi-natural conditions. Under natural conditions this has been shown by Orgain and Schein (1953) with rats and by Brown (1953) with house mice.

That population size and competition are important in determining spatial distribution is evident from Calhoun's (1950) study of a freely growing rat population in a quarter acre enclosure structured to provide a gradiant of availability to the food. Rats born near the source of food were able to maintain more effectively their home areas and force animals living in submarginal areas to remain there. Stability of spatial distribution related to numbers of animals in an area is evidenced by experiments in which part of the population was removed. Stickle (1946) and Blair (1940) with Peromyscus, Orgain and Schein (1953), with rats, and Calhoun and Webb (1953) with several species of small mammals demonstrated the tendencies of animals living in surrounding areas to move into vacated areas following the removal of the residents. Animals released into areas already populated by members of the same species rapidly dispersed (Blair, 1940; Calhoun, 1948) or disrupted the population and this resulted in a temporary decrease in the population numbers (Davis and Christian, 1956).

Purely social factors influencing spatial distribution will be discussed later. It should be remembered, however, that the separation of the discussion of such factors does not mean that they operate independently of those mentioned above. All factors influencing spatial distribution in local and geographical populations probably operate simultaneously although at any point in time they may control populations singly (Leopold, 1933, p. 38).

STATEMENT OF THE PROBLEM

The nature of the social factors influencing spatial distribution in local populations of small mammals has not been clearly demonstrated.. Individual differences in social behavior may influence the establishment and maintenance of patterns of distribution.

Calhoun (1949, 1950, 1952) studied rats (Rattus norvegicus) in a 100 foot square area surrounded by a rat proof fence. The field was structured to produce a gradient of availability to the food. Rats living in the alleys which adjoined the food were in a more favorable food situation than those rats living farther away. To get food, the rats living at a distance from the food source, were forced to pass through the home areas of the rats living closer to the food. Rats living close to the food grew more rapidly, and since weight is an important factor in attaining high social rank, they were more favored in attaining higher social status than their peripheral neighbors who got less food and grew more slowly. The social status of the peripheral rats was passed on to the later generations. Smaller adults were forced into the peripheral areas of the enclosure. Their young, because they were born distant from the food source, grew slowly and thus were relegated to a low social status.

Calhoun (1956) studied the effects of behavioral differences upon population dynamics where genetic factors were controlled. He studied freely growing populations of Mus musculus, using the two genetic strains DBA/2 and C57Bl/10 which differ in physiological and behavioral characteristics. His study was drastically curtailed since there was extremely poor reproduction among DBA/2 mice. He showed, however, that physiological disturbances resulting from the poor adjustment of the mice to new situations, including relations with other individuals, were more prevalent in the DBA/2 mice. His results indicated that as population density increased, social differences due to genetic factors may have been differentially expressed in the physiology of the individual mice.

King and Eleftheriou (1957) raised Peromyscus maniculatus bairdii in the laboratory in isolation or in groups of six individuals from weaning until 60 days of age. Following this social treatment, the mice were released into an isolated field containing nest boxes and live traps in an effort to discover any differences in their ability to adapt to the natural environment. Subsequent to release, isolates moved about the field more and at greater distances than group raised mice. Group raised mice were found together more frequently than the isolation raised mice. These results were difficult to evaluate, however, since the popu- declined rapidly after release.

One social factor offered to explain spatial patterns of distribution in small mammals is territoriality, defined as defense of an area (Noble, 1939). While territorial behavior is of widespread occurrence in birds (Howard, 1920;

Nice, 1941), such behavior in small mammals is a matter of controversy (Blair, 1953; Burt, 1940; 1943, 1949; Crowcroft, 1955; Scott, 1944). If territoriality does exist as a characteristic mechanism maintaining spatial distribution relative to the physical environment and the biology of most species, what social factors are important in the establishment and maintenance of such behavior? If territoriality is not characteristic of all species, what social mechanisms effectively regulate spatial patterns of distribution in non-territorial species? Do differences in the social behavior of the individual animals of the population affect spatial distribution?

This study was designed to combine laboratory and field techniques in order to examine the significance of social factors in the spatial distribution of Prairie Deermice within local populations.

The objectives of this study were:

1. To study the affect of social manipulation of deermice populations in the laboratory upon their subsequent spatial distribution in a semi-natural environment.
2. To examine behavior patterns effecting spatial distribution in free ranging, semi-natural populations.
3. To measure the individual awareness of and preference for the home area as well as the stability of such an area.

MATERIALS

Experimental Animals

The Prairie Deermouse (Peromyscus maniculatus bairdii, Hay and Kennicott), inhabits prairies, open fields, beaches and dense grass along fence rows in the midwestern United States. It does not occur in Maine, where this study was conducted, although, another subspecies, Peromyscus maniculatus abietorum, is found in the Spruce-Fir forest surrounding the study area on Mount Desert Island. P. m. bairdii was selected as the experimental animal because quantities were available from a laboratory colony, and a grassland form was considered better suited to the study contemplated. No native grassland species of Peromyscus occur in Maine. An attempt was made to correct for any ecological imbalance between the maritime environment and the adaptability of this subspecies by providing food, nest sites and nesting material in excess of need. The biology of the experimental mice in terms of reproduction, weight, general body condition, and survival indicated that this attempt was successful, at least for the short periods under study.

All of the mice were born in the laboratory and most were born in a single colony of 60 breeding pairs. These were descendants of twelve original pairs whose offspring had been in the laboratory for approximately 15 generations.

Although natural populations of Prairie Deermice have been extensively studied (Blair, 1940; Dice, 1932; Howard, 1949), the factors involved in the spatial distribution of local populations are unknown. Burt (1949) suggested that territoriality is a part of the behavioristic pattern of many kinds of animals and results in population dispersal. On the basis of live trapping and nest box studies of wild populations, Blair (1940, 1953) and Howard (1949) concluded that P. m. bairdii does not show antagonistic behavior and thus is nonterritorial in the defined sense. Howard (ibid), however, postulated that Prairie Deermice exhibit some kind of natural negative response to crowding beyond a certain density within a limited area, but he was not able to describe, measure, or demonstrate the existence of any such negative force.

Laboratory Facilities

The laboratory phase of these experiments involved no manipulation other than keeping the mice in specific social situations under conditions of light, temperature and humidity similar to those to which the complete laboratory breeding colony was subjected. The social situations and materials used will be discussed in the appropriate procedural sections.

All of the mice were kept in basement rooms in the Behavior Division of the Roscoe B. Jackson Memorial Laboratory. Lights were on in these rooms from approximately 7:30 A.M. to 4:30 P.M. each day. Each mouse was housed in a single compartment of a two compartment mouse box described in the discussion of the social treatments. Purina laboratory pellets and water in excess of need were provided by means of a food hopper and water bottle in the lid of each box. The floor was covered with a thin layer of wood shavings, and the mice were placed in other, clean nest boxes every two weeks.

Experimental Field

General Description

The experimental area was a 0.9 acre field located approximately 150 yards north of the Hamilton Station of the R. B. Jackson Laboratory. The field was 250 feet long and 165 feet wide with the length having a compass bearing of NE - SW. A gradual slope in the longitudinal direction from SW to NE caused runoff of water toward the NE end during heavy rains. The vegetation was predominantly herbaceous, although forbs were found in quantity in parts of the field.

The experimental area was one of three one-acre fields. In 1945, all trees of the Spruce-Fir forest were cleared from the area, and the soil smoothed. No attempt was made to level or dump fill in the area. The northeast end of the field was soggy due to poor internal drainage and the runoff of water from the elevated southwest end.

Design

Enclosure. When originally constructed for dogs, the experimental field was surrounded by a seven feet high wooden fence to which wire fencing was attached at the bottom and buried in the ground. This made the enclosed area dog and fox proof. The northern part of this fence suffered severe wind damage prior to the start of the study reported here and approximately thirty feet were replaced by a wooden fence four feet high.

A map of the experimental field is shown in Figure 2. The area was divided into two 0.44 acre plots, each 240 feet by 80 feet and surrounded by corrugated aluminum partially buried on edge in the ground (Figure 3). The rolls of aluminum measured 100 feet by 28 inches and were buried to a depth of 8". Flat pieces of aluminum placed horizontally were wired to the enclosure to prevent escape where two pieces of aluminum fencing met (Figure 4). Since the two plots were adjacent, a single piece of aluminum served as a common inside boundary for each.

The eastern plot was designated as Plot A and the western one as Plot B. Nest boxes and live traps were placed in an identical pattern in each plot as shown in Figure 2. Due to an observation booth previously built into the wooden fence, files A and B were 18 feet and 6 feet shorter respectively than the other files. Thus, in file A there was one less trap station than found in the others.

Nest boxes. Twenty-four subterranean nest boxes represented by circles in Figure 2 were placed in each plot along three files and eight ranks. In Plot A these files were B, D, F, and in Plot B they were T, W, and Y. The even numbered ranks indicated nest boxes in both plots. Each nest box was 30 feet from its nearest neighbor in the same file or rank. Nest boxes in files B and F in Plot A and T and Y in Plot B were 10 feet from the longitudinal aluminum fence nearest

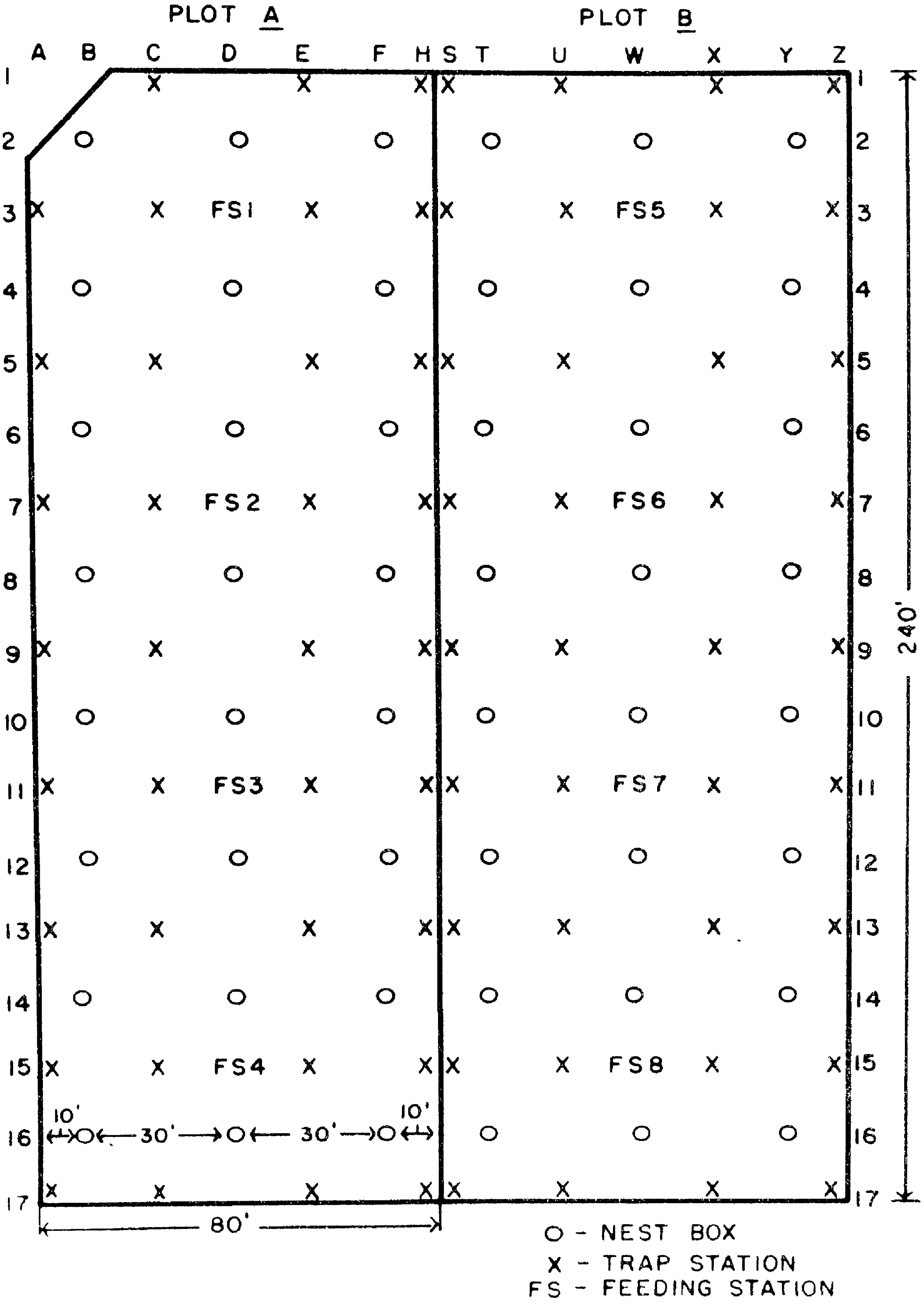

Fig. 2. Design of the experimental field.

Fig. 3. North-east view of the experimental field.

Fig. 4. North-east view of the experimental field along the partition between plots.

them. The end nest boxes in each plot were 15 feet from the end fence.

Each nest box (Figure 5) was built of one-half inch lumber, and had the following outside dimensions: 6½" wide x 5-3/4" deep x 7" high. The nest chamber was floored by a piece of 3/8" hardware cloth supported 1¼" above the inside floor of the box, and roofed by a ceiling of hardboard 3" above its own floor. Thus, it measured 5½" x 4-3/4" x 3". An air space of 1" for purposes of insulation was present between the ceiling of the nest chamber and the inside surface of the lid of the nest box. A 6" piece of white rubber laboratory hose of 1¼" outside diameter was connected to an opening centered 2½" above the floor of the nest chamber. This arrangement provided a pliable entrance tunnel of 1" inside diameter which was small enough to prevent larger animals from entering the box and was completely waterproof when snugly attached. Each nest box was thoroughly saturated with paraffin and the hose entrance tunnel was heavily coated at the point of connection with the box. This method of preparing the boxes was effective in providing a waterproof nest site for the mice.

Each nest box was completely buried in the ground. The top was covered by a piece of heavy roofing material and a large piece of sod. These provided additional insulation.

Cotton batting was used as nesting material. Six different colors were used in order to obtain a measure of the transportation of nesting material and were placed in the

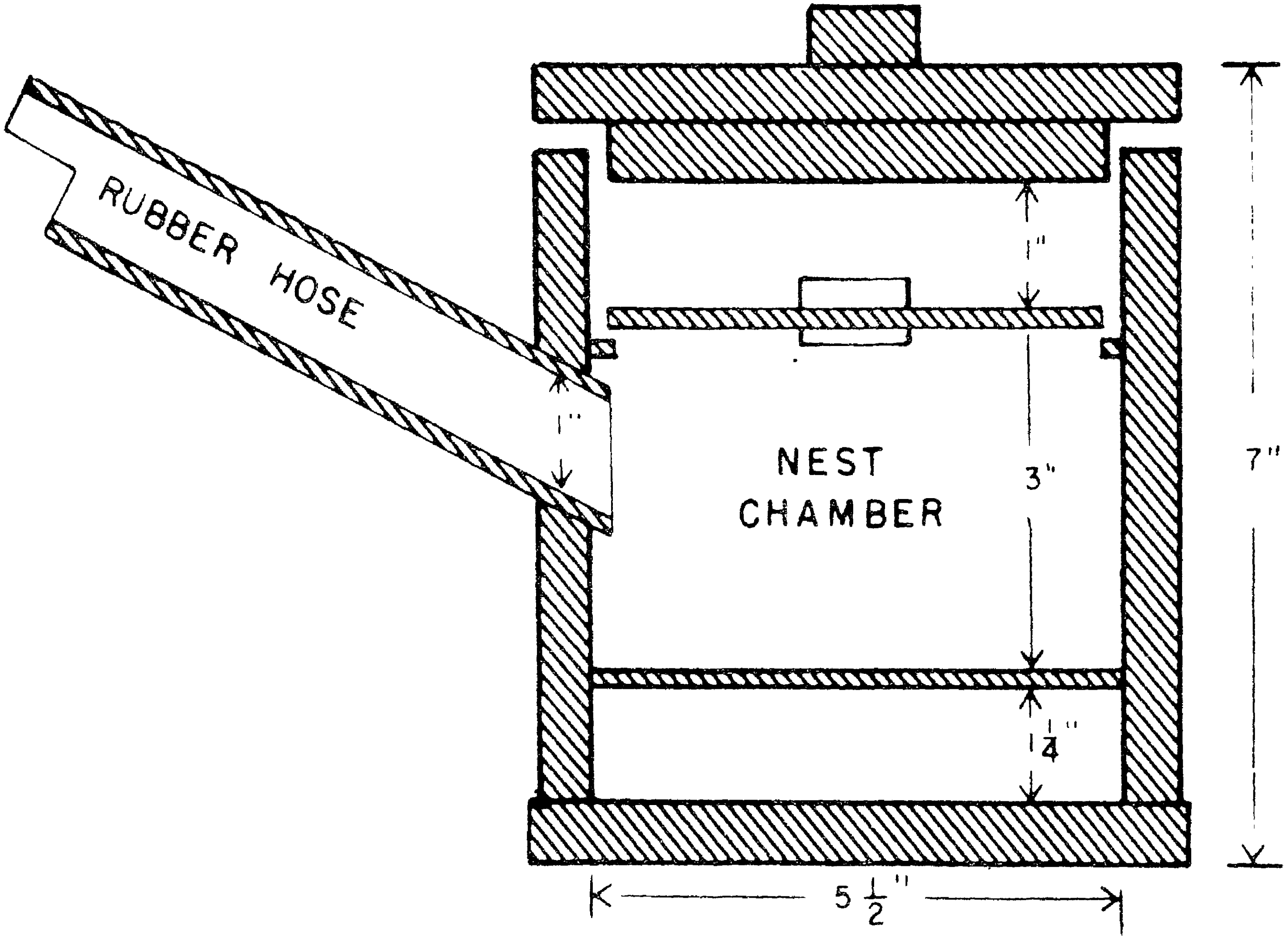

Fig. 5. Diagram of a nest box.

nest boxes in the following pattern:

Files	Boxes	
	2, 6, 10, 14	4, 8, 12, 16
T & B	Red	White
W & D	Blue	Green
Y & E	Purple	Yellow

There was, however, little evidence of such transportation during the period reported here.

The mice used nest boxes almost exclusively and there was little indication of nesting in the field and subsequent sporadic use of the nest boxes as reported in some other studies (Nicholson, 1941; Howard, 1949; King, 1957).

Live traps. There were four files of trap stations (X in Figure 2) alternating with the files of nest boxes in each plot. Due to the previously mentioned variation in the eastern outside boundary of Plot A, there were only 35 trap stations in this plot while Plot B contained 36. Two live traps were placed at each trapping station within the area enclosed by the aluminum fence. At each marginal trap station, one additional trap was located outside the aluminum fence and was left set continually. Thus, a total of 169 live traps were used in the experiments, of which 27 were located outside the enclosure.

Each live trap was a rectangular box, 9" long x 3" wide x 3" high, the sides and top of which were made of galvanized sheet metal and the floor of 3/8" plywood. The hardware cloth door was supported by a wire attached to a treadle. When a mouse stepped on the back half of the treadle, the support was removed and the door fell, releasing a lock which prevented the trapped mouse from opening the door or entry by other mice.

Feeding stations. Food was provided in excess of need in the field and was placed in a small hardware cloth food hopper to prevent hoarding. One food hopper was placed at each of four feeding stations (**FS in Figure** 2) in each plot located at the intersections of files **D** and **W** with ranks 3, 7, 11, and 15. The feeding stations remained in the field at all times and were distributed equidistant from the nearest nest boxes.

Each feeding station (Figure 6) was provided with a mechanism for recording time and frequency of visits by the mice. When a mouse traveled to or from the food hopper, a pen attached to a treadle, which was part of the ramp leading to the food, was brought into contact with a continuous 1" wide paper tape. A spring-wound clock powered a large spool which wound tape from a reservoir spool containing enough for 48 hours of recording. Two different colors of Esterline-Angus ink were used so that tapes could be exchanged between recorders and a single tape used for a longer period of time.

Lights. Light for nocturnal observations was provided by seven 150 watt flood lights attached twelve feet above the ground to posts located along file H at ranks 3, 5, 7, 9, 11, 13, and 15 (Figure 4).

A headlight powered by 4 standard size flashlight batteries was used when the floodlights were not desired.

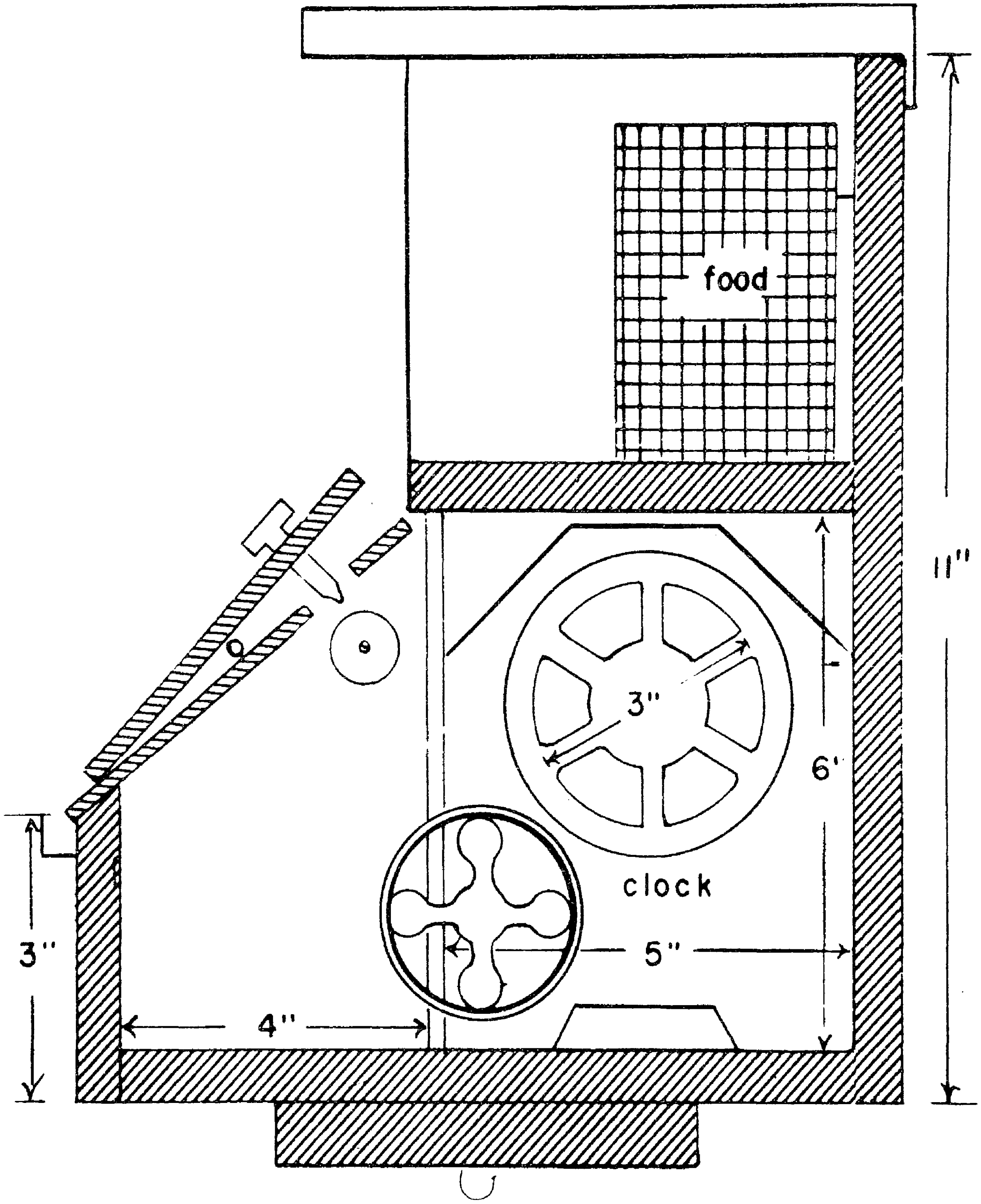

Fig. 6. Diagram of a feeding station.

Weather station. A small weather station (Figure 4) was attached one foot above the ground to the light post at H-9 in Plot A. The station was a wooden box 24" wide x 8" deep x 18" high with a roof covered with asphalt roofing. The box was painted white and the front which faced the southwest was louvered. A 24-hour recording thermograph, a wet-dry thermometer, and a maximum-minimum thermometer were placed inside the weather station. Barometric recordings and additional temperature recordings were made on apparatus set up a short distance from the experimental field.

Vegetation Analysis

Species list. A total of 66 species of plants from 28 families were identified from the experimental field and are listed in Table II.

Plant distribution. Plant distribution in the plots was ascertained by recording species present in meter square areas near the nest boxes in each plot. A meter square quadrat was systematically placed to the east of nest boxes in files D and F in Plot A and files W and Y in Plot B and to the west of file B in Plot A and file T in Plot B. The difference in sampling direction was necessary because of the proximity of files B & T to the aluminum fence.

At each nest box the investigator took one stride in the proper direction, held the quadrat at arm's length and then dropped it. All plants emerging from the soil within the quadrat-circumscribed area were recorded. Table III lists those species recorded in at least 5 of the 24 quad-

TABLE II

PLANTS RECORDED IN EXPERIMENTAL FIELD

Family	Scientific Name	Common Name
Musci	Sphagnum sp.	
Equisetaceae	Equisetum arvense	Common Horsetail
Gramineae	Agrostis alba	Redtop
	Calamagrostis canadensis	Blue-joint
	Festuca rubra	Fescue-grass
	Holcus lanatus	Velvet grass
	Phleum pratense	Common Timothy
Cyperaceae	Carex sp.	Sedge
	Eleocharis obtusa	R. Br. Spike-Rush
	Eleocharis tenuis	Spike-Rush
	Scirpus rubrotinctus	Bulrush
Juncaceae	Juncus brevicaudatus	Rush
	Juncus bufonius	Toad-Rush
	Juncus effusus	Soft Rush
	Juncus tenuis	Rush
	Luzula multiflora	Woodrush
Iridaceae	Iris versicolor	Blue Flag
	Sisyrinchium angustifolium	Blue-eyed grass
Orchidaceae	Spiranthes romanzoffiana	Hooded Ladies'-Tresses
Corylaceae	Alnus crispa	Green Alder
Polygonaceae	Polygonum persicaria	Lady's-thumb
	Rumex acetosella	Sheep-sorrel
Caryophyllaceae	Stellaria graminea	Common stitchwort
Ranunculaceae	Ranunculus acris	Tall Buttercup
Droseraceae	Drosera rotundifolia	Round-leaved sundew
Rosaceae	Fragaria virginiana	Strawberry
	Potentilla canadensis	Five-finger
	Rubus hispidus	Dewberry
	Rubus idaeus	Rasberry
	Rubus sp.	Bramble

TABLE II - Continued

Rosaceae	Rosa virginiana Spiraea latifolia	Rose Meadow Sweet
Leguminosae	Trifolium agrarium Trifolium pratense Vicia cracca	Yellow Clover Red Clover Tufted Vetch
Oxalidaceae	Oxalis europaea	Wood-sorrel
Rhamnaceae	Impatiens capensis	Spotted Touch-me-not
Guttiferae	Hypericum canadense Hypericum perforatum	St. John's-Wort Common St. John's-Wort
Cistaceae	Lechea intermedia	Pinweed
Violaceae	Viola sp.	Violet
Onagraceae	Epilobium angustifolium	Willow-herb
Ericaceae	Vaccinium angustifolium	Low Sweet Blueberry
Labiatae	Galeopsis tetrahit Lycopus uniflorus Prunella vulgaris	Hemp-nettle Water Horehound Heal-All
Solanaceae	Solanum dulcamara	Bittersweet
Scrophulariaceae	Rhinanthus crista-galli Veronica officinalis	Yellow Rattle Common Speedwell
Plantaginaceae	Plantago lanceolata Plantago major	Ribgrass Common Plantain
Caprifoliaceae	Diervilla lonicera	Bush-honeysuckle
Compositae	Achillea millefolium Aster lateriflorus Aster simplex Aster umbellatus Chrysanthemum leucanthemum Cirsium Gnaphalium uliginosum Hieracium aurantiacum Hieracium canadense Hieracium flagellare Hieracium pratense Leontodon autumnalis Solidago bicolor Solidago graminifolia	Common Yarrow Aster Aster Aster White Daisy Common Thistle Low Cudweed Orange Hawkweed Hawkweed Hawkweed King Devil Fall Dandelion White Goldenrod Goldenrod

Taxonomy after Fernald (1950)

TABLE III

TABULATION OF OCCURRENCE IN QUADRATS OF ALL SPECIES RECORDED IN AT LEAST FIVE QUADRATS

Plant Species	Plot A	Plot B
Sphagnum sp.	7	1
Agrostis alba	20	17
Festuca rubra	24	24
Holcus lanatus	5	2
Carex sp.	7	15
Juncus sp.	9	2
Luzula multiflora	13	10
Sisyrinchium angustifolium	8	8
Stellaria graminea	8	3
Fragaria virginiana	2	12
Potentilla canadensis	15	13
Spiraea latifolia	8	8
Trifolium agrarium	10	4
Trifolium pratense	20	8
Vicia cracca	6	0
Oxalis europaea	0	5
Viola sp.	1	9
Prunella vulgaris	7	2
Rhinanthus crista-galli	9	2
Veronica officinalis	7	6
Achillea millefolium	6	3
Aster lateriflorus	13	18
Hieracium sp.	9	18
Solidago graminifolia	5	12
Leontodon autumnalis	5	3

rats sampled in either Plot A or B. The number of quadrats in which each species was found is also given. There was a wider distribution of the plant species in Plot A than in Plot B.

Table IV shows the distribution of the plants recorded in 5 or more quadrats in at least one of the plots. Since each sample was taken in conjunction with a nest box, the presence of each species is recorded by nest boxes. The pattern of distribution shows a similarity between plots with the moisture loving plants occurring in the wetter northeast end of the plots in the areas of nest boxes 12, 14, and 16.

Standing crop. A measure of the distribution of plant mass in each plot was taken late in September, 1958, (Experiment 6). One cubic foot samples of plant material were taken every 15 feet along each of the three files of nest boxes in each plot. Samples were taken in the same direction from files of nest boxes as was done when sampling the distribution of plant species. All plant material within the one cubic foot of volume enclosed by the quadrat was clipped at a height of 1" above the ground, placed in a paper sack and transported to the laboratory.

The sampled plant material from each quadrat was kept in the laboratory for a minimum period of one week. Subsequently, all samples from one transect in each plot were placed in an electric oven for 48 hours at a temperature of 50 degrees Centigrade. The samples remained in the paper sacks during drying and this procedure was repeated for all

TABLE IV

THE DISTRIBUTION OF PLANT SPECIES IN THE EXPERIMENTAL FIELD

PLOT A

	B 2	D 2	F 2	B 4	D 4	F 4	B 6	D 6	F 6	B 8	D 8	F 8	B 10	D 10	F 10	B 12	D 12	F 12	B 14	D 14	F 14	B 16	D 16	F 16
Sphagnum sp.																	X		X	X	X		X	X
Agrostis alba		X	X		X	X		X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X
Festuca rubra	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Holcus lanatus	X												X			X			X			X		
Carex sp.																	X	X			X	X	X	X
Juncus sp.	X				X						X	X									X	X	X	X
Luzula multiflora					X			X	X	X	X	X		X		X	X	X	X	X		X		
Sisyrinchium angustifolium											X					X	X		X	X	X		X	X
Stellaria graminea				X	X		X	X		X			X			X			X					
Fragaria virginiana									X									X						
Potentilla canadensis							X	X		X	X		X	X	X	X	X	X	X	X	X	X	X	
Spiraea latifolia									X		X			X	X			X	X	X			X	X
Trifolium agrarium				X	X		X	X		X	X		X			X				X	X			
Trifolium pratense	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X			X	
Vicia cracca				X			X	X		X			X	X										
Oxalis europaea																								
Viola sp.																								X
Prunella vulgaris					X						X	X					X	X	X	X				
Rhinanthus crista-galli	X			X	X			X			X			X		X	X				X			
Veronica officinalis			X				X				X	X		X					X	X				
Achillea millefolium	X				X			X		X			X						X					
Aster lateriflorus					X				X	X	X	X	X	X	X	X		X		X	X		X	X
Hieracium sp.			X				X			X	X		X	X		X			X			X		
Solidago graminifolia									X		X	X							X	X				
Leontodon autumnalis	X	X	X	X																				X

TABLE IV - Continued

PLOT B

	T 2	W 2	Y 2	T 4	W 4	Y 4	T 6	W 6	Y 6	T 8	W 8	Y 8	T 10	W 10	Y 10	T 12	W 12	Y 12	T 14	W 14	Y 14	T 16	W 16	Y 16
Sphagnum sp.																								X
Agrostis alba	X	X		X	X	X	X	X	X	X		X	X	X	X	X	X		X	X		X		X
Festuca rubra	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Holcus lanatus	X					X																		
Carex sp.				X			X			X	X		X	X	X	X	X	X	X	X		X	X	X
Juncus sp.											X								X			X		X
Luzula multiflora		X								X	X		X			X		X		X	X		X	X
Sisyrinchium angustifolium											X		X	X		X	X	X						X
Stellaria graminea		X			X																X			
Fragaria virginiana					X		X			X	X				X		X	X	X	X	X		X	X
Potentilla canadensis		X		X			X	X	X	X	X				X	X			X	X	X		X	
Spiraea latifolia							X			X			X			X		X	X		X			X
Trifolium agrarium							X		X		X													X
Trifolium pratense		X	X				X			X	X		X				X			X				
Vicia cracca																								
Oxalis europaea					X	X			X									X			X			
Viola sp.					X									X	X		X	X			X	X	X	X
Prunella vulgaris										X			X											
Rhinanthus crista-galli				X						X														
Veronica officinalis					X					X	X			X				X	X					
Achillea millefolium										X					X				X					
Aster lateriflorus	X	X	X				X	X	X	X	X		X	X	X	X	X	X	X	X	X		X	X
Hieracium sp.	X	X	X		X	X	X	X	X	X	X	X		X	X	X	X	X		X	X		X	X
Solidago graminifolia		X					X	X	X		X		X	X	X	X		X	X		X			
Leontodon autumnalis						X			X														X	

samples. Immediately following the drying period, the samples were weighed to the nearest gram. An analysis of variance was performed between plots and the calculated F value of 5.6 with 68 degrees of freedom was significant at the 5% level. Thus, Plot B had a significantly greater mass of vegetation than Plot A.

Figure 7 indicates the distribution of the weights of vegetation obtained by the cubic foot sampling method and grouped into three weight classes. Since the samples were taken only along the files of nest boxes, the weight class indicated by each sample was extended one-half the distance to the nearest sample in all directions. This resulted in an artificial distribution pattern, the accuracy of which decreased as the trap lines were approached.

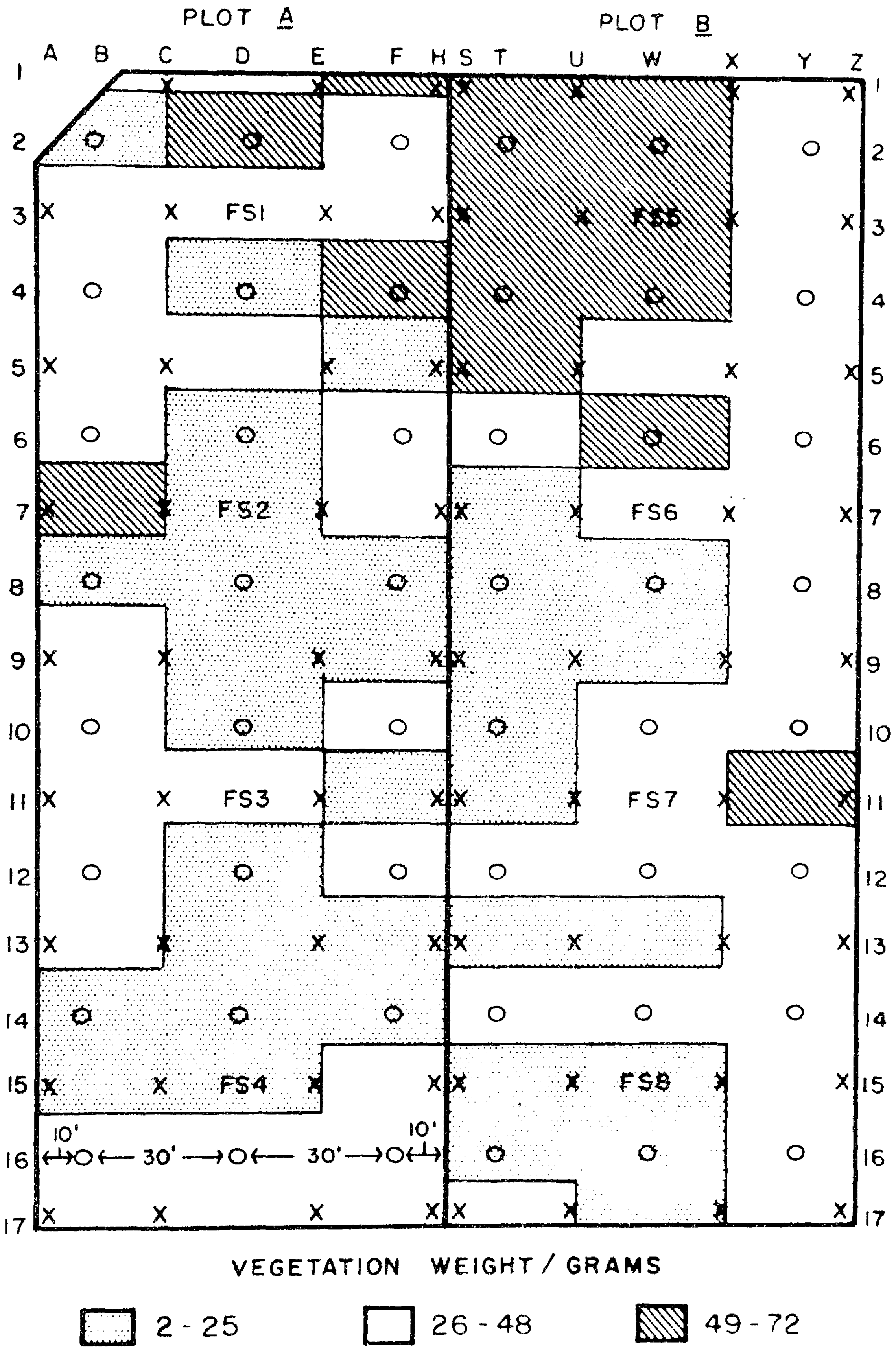

Fig. 7. The distribution of plant mass.

PROCEDURES

This research was designed as a study of the affects of social manipulation in the laboratory upon the spatial distribution of Prairie Deermice subsequently living in semi-natural field conditions. There were eight experimental periods, each of three weeks duration between June 6 and November 21, 1958. During this time 8 populations of four bisexual paris raised either in isolation or in groups were living in each of the two plots of the experimental field (Figure 2). Thus, the total number of mice released into the plots was 128 of which 64 were raised under each of the two social treatments.

The procedures utilized generally may be placed into three categories designated as laboratory, field, and a combination of the two. A discussion of general procedures also includes others not readily placed in the above categories.

Laboratory Procedures

Social Treatments

All mice were born in the laboratory and remained with their parents until weaning at three weeks of age. Each family occupied one compartment of a standard two compartment mouse box. Each compartment was 6" x 11" x 6" in size, and food and water were provided through a food hopper and water bottle in the cover. Litters were selected for social treatment by the following criteria: birth must have occurred within a nine day period centered around a day 70 days prior to the scheduled day of release into the experimental field; each litter must have contained at least one male and one female; and both parents must have survived until the date of weaning.

At three weeks of age, the young mice were separated from their parents and randomly placed either in a group or in isolation.

Isolation raised mice. Isolation, as used in this study, refers to a single mouse living in one compartment of a standard mouse box (Figure 8) from weaning at three weeks until ten weeks of age. Visual and tactual contact with other mice during the treatment period was thus prevented. In all cases male and female sibs lived in the different compartments of the same box.

Group raised mice. The group social treatment differed from the isolation treatment in two ways. First, the partition separating the two compartments in each mouse box used in the group treatment was made of ¼" hardware cloth instead of wood as in the isolation boxes (Figure 8). Secondly, a male and female were placed in each compartment of each box. All four mice assembled in each mouse box were strangers to each other and were young from four different litters. A male and female from one litter were cross-paired with a male and female from another litter and the two cross-litter pairs thus formed were placed in two different mouse boxes. Each mouse in the group situation had tactual contact with one other mouse, its pair-mate, and visual contact with the three

Fig. 8. Mouse boxes used in the two social treatments. Left - Group Raised; Right - Standard box - Isolation Raised.

mice in its box. Figure 9 illustrates the procedure for placing mice in the social treatments.

The group situation was devised to assure, as nearly as possible, similar social development of successive populations of group raised animals at the time of their introduction into the field. The unpredictability and difficulty of measuring social hierarchies, dominance-submission, etc., which exist in larger groups, were considered sufficient to necessitate as rigid control of social interaction as possible.

During the treatment period, food and water were supplied in excess of need and the animals were moved to other, clean mouse boxes every two weeks. Both treatment populations were kept in their respective social situations until release into the field at ten weeks of age. At this age the mice were physically and reproductively mature (Clark, 1938; Dice and Bradley, 1942).

Preparation of the Mice for Release

At ten weeks of age, (Figure 9) eight mice from each social treatment were released into different one-half acre plots of the experimental field. Animals to be released were selected according to two specifications. First, no pregnant females were acceptable. Pregnancy was ascertained by inspection and palpation. Second, populations released in the field were composed of a male and a female from each of four litters. For the isolation raised mice, this was accomplished by random selection of four mouse boxes each containing a male and female. As indicated previously, group raised males and females were raised as cross-litter pairs. Thus, random

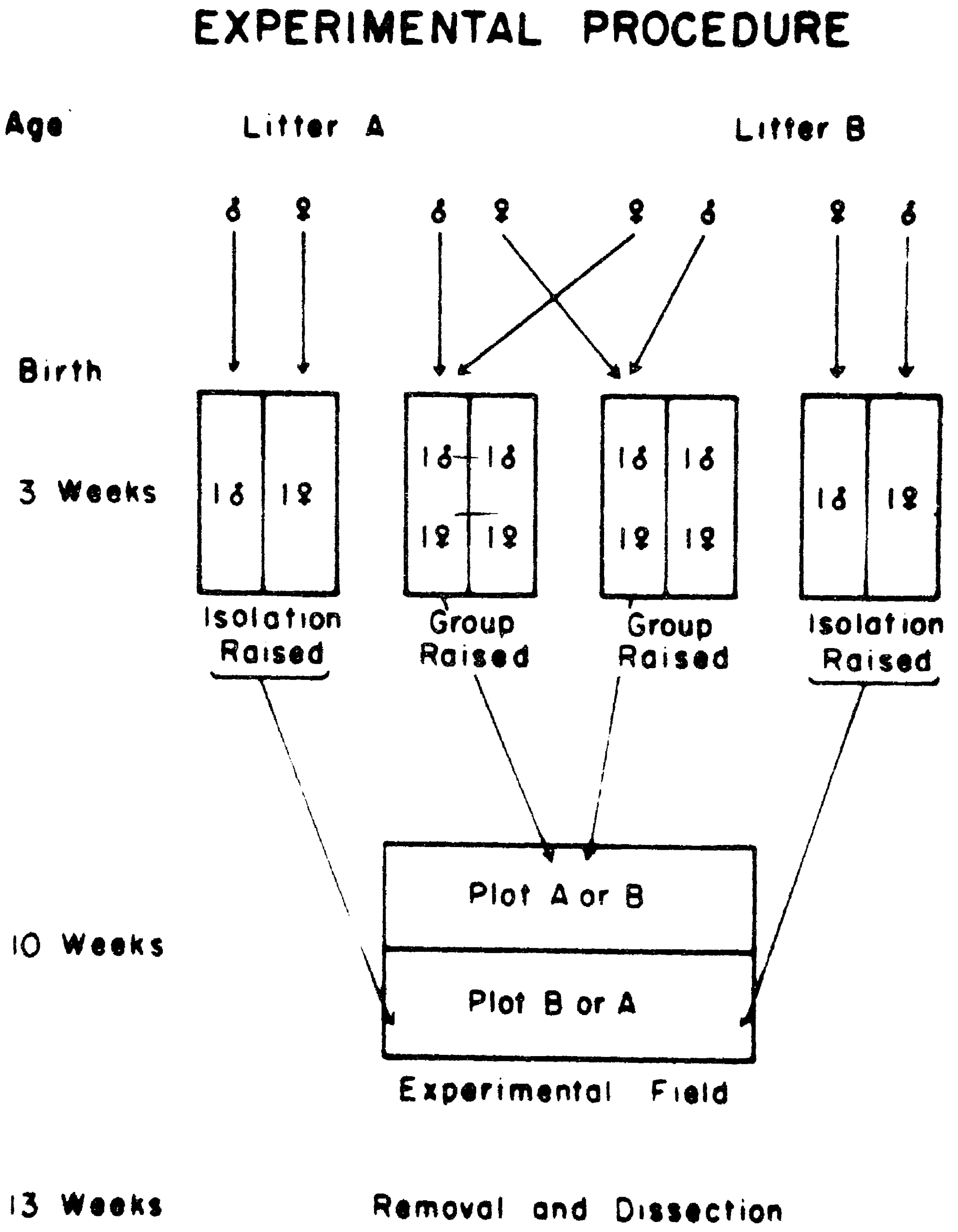

Fig. 9. Hypothetical experimental procedure. All litters did not contain 2 males and 2 females. Thus, the same litters were not represented in both treatment groups.

selection of one pair necessitated the selection of the reciprocal mating involving the sibs of the first pair selected. Only one of the two pairs living in a single group mouse box was released into the field.

Henceforth, in this discussion, those mice which were introduced into the field shall be referred to as experimentals and those remaining in the laboratory in their original social treatment as controls.

On the day preceding scheduled introduction into the field, both the experimentals and controls of each social treatment were etherized, weighed, and numbered by toe clipping. In addition, all experimental mice were tagged with a numbered fingerling tag which was used to attach a colored celluloid disc to one ear. Immediately after weighing and tagging, the isolation raised experimentals were returned to their boxes where they remained in isolation until release into the field. Following weighing and tagging, each pair of group raised experimentals was placed in a different group-treatment mouse box. The individuals of each pair were separated and placed, one in each compartment. Since only one pair of group raised mice was selected for the field from any single group box, recombinations of the control mice were made to fill the vacant compartments. This was done by moving pairs in from other partially vacated group boxes.

Field Procedure

Preparation of the Experimental Field

Prior to the introduction of each experimental population, the nest boxes in each of the plots were cleaned and clean cotton nesting material and five pellets of Purina laboratory mouse food were placed in each nest box.

Introduction of the Mice to the Field

The experimental mice were released in the field at least one hour before sunset on the same day that the previous populations were removed. This was also true for the first experiment since preliminary populations preceded it. Release of populations raised in each social treatment alternated between plots A and B for successive experiments. The experimental populations were introduced into the plots as systematically as possible since preliminary work indicated that releasing the populations at the center of each plot resulted in high mortality. Thus, a pattern of introduction into nest boxes was followed for each plot and was repeated for the eight experimental periods. This pattern of introduction is illustrated in Figure 10.

Assignment of the experimental mice to nest boxes was done by using the most closely associated pairs as the basic units for distribution. The isolation treatment was represented by 4 sib-pairs of mice with the individuals of each pair having been raised in separate compartments of the same mouse box. The most closely associated group raised pairs were not sibs as in the case of the isolates, but were mice

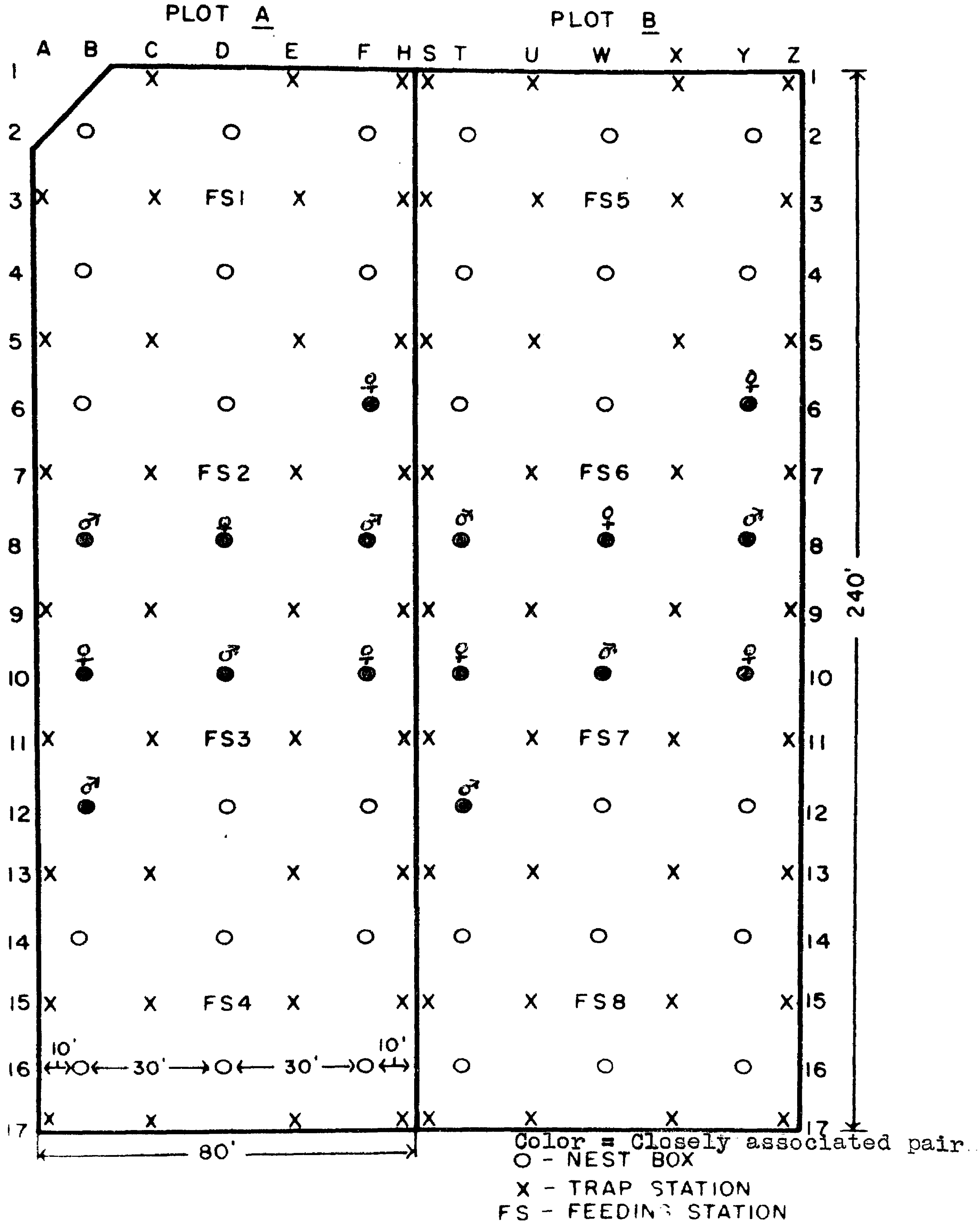

Fig. 10. Patterns of introduction of the mice into the plots.

living together since weaning. Males and females of each closely associated pair were released into nest boxes separated from each other by a distance of 67.1 feet. In addition the pattern of introduction of the animals of each population was such that the nearest neighbors of the same sex were separated by a distance of 42.4 feet and those of the opposite sex by 30 feet. This procedure assured that:

(a) Naive animals gained experience with one nest box.

(b) Original distribution patterns were constant for each experimental population no matter into which plot it was placed.

(c) Individuals of all closely associated pairs were initially equidistant from each other.

(d) All mice were equidistant from the nearest neighbor of the same sex.

(e) All mice were equidistant from the nearest neighbor of the opposite sex.

Period of Population Establishment

Following introduction into the field, a period of 17 days was considered sufficient for the mice to establish themselves in a relatively stable manner in the field. The 17 day period was set arbitrarily and was considered adequate after inspection of data collected in preliminary experiments.

Daily records. During the "period of establishment", daily checks of all nest boxes in each plot were made and the whereabouts of each mouse recorded. No time schedule was followed for checking the nest boxes in each field, and since all mice wore a celluloid disc of a different color on one ear, it was not necessary to handle them for identification.

The procedure was to open the box, push the cotton aside, and record the mice present. Rarely, mice jumped from the nest and tried to escape. They were caught, if possible, and returned to the nest box. It was interesting to note that escape behavior most frequently occurred among animals recently released in the field or among those that had escaped or tried to escape at previous inspections. If animals were prevented from escaping during the first two nest box checks following introduction, very few made escape attempts during subsequent inspections.

Trapping periods. Two periods of live trapping were conducted during each experiment's "period of establishment". Each trapping period was of four nights' duration and on each night, traps remained set until two hours after sunset. The first trapping period began on the second night the mice were in the field and continued through the fifth night after introduction. The second trapping period was conducted on the 14th, 15th, 16th, and 17th nights of each period of establishment. On the night preceding the first trapping period, the traps were baited and turned upside down permitting the mice to enter and obtain the food without capture. A single pellet of Purina laboratory mouse food was used as bait in each trap during the prebaiting as well as in the regular trapping period. Traps were set at various times during the day but were checked and unset at two hours after sunset each trap night. Mice were released by turning the traps over and allowing them to escape or by shaking them into a plastic sack and then releasing them. Each mouse was recorded by its number as indicated by the colored ear disc and combination of toes clipped. Subsequent to each trap check the traps were turned over, baited with a single pellet of food, and left open so that mice could enter and not be caught for the remainder of that night. On the day following each trapping period, the bait was removed from each trap and the traps were unset, although they remained open and accessible to the mice.

Combination of Laboratory and Field Procedures

Homing

Homing was defined in this study as the ability of individual animals to return to previously occupied nest boxes in an experimental plot after being absent from the plot and nest boxes for approximately 36 hours. Decision was made to use this homing test to measure the ability of the mice to home; measure the significance of previously established spatial distribution patterns; and provide basic data from which to make comparisons of homing ability when the home nest boxes were empty and also when aliens were in the home nest boxes.

Establishment of the homing phenomenon. On the morning of the 17th day following the introduction of the populations into the field, all mice were removed from the experimental plots. Each was taken from a nest box at approximately 8:00 A.M., placed in a live trap, transported to the laboratory, and kept in isolation in a standard mouse box until sunset of the following day. Thus, each animal was in the laboratory for approximately thirty-six hours during which food and water were supplied in excess of need. Rarely, all mice known to be in the field were not found on the morning they were scheduled to be removed and thus could not be taken to the laboratory for the total isolation period. In this event, the live traps in the plot were set that evening and the animals were taken to the laboratory when caught.

Following the thirty-six hours of isolation, each experimental animal was reintroduced to its home plot at a point distant to the area of its most frequent previous occurrence. Following the technique of Hayne (1949) for calculating the center of activity from trap data, a "Residence Center" was calculated for each animal, using nest box records obtained during the last 10 days preceding removal from the field. The field was bisected transversely and mice whose residence centers occurred in one-half of the field were reintroduced at the release point in the opposite half. In Plot A, the release points were feeding stations 1 and 4 and in Plot B they were feeding stations 5 and 8 (Figure 2).

Reintroduction to the field was made at sunset of the day following removal. The mice were taken from the laboratory in live traps and at the appropriate release points the traps were turned over and left on the ground. The investigator immediately left the area and the mice could leave the traps at any time.

Homing with aliens temporarily in the field. A single alteration in the homing test was made for Experiments 6, 7, and 8. During previous tests all nest boxes in each plot were empty at the time of the reintroduction of the experimental mice. Beginning with experiment 6, however, the plots were transversely bisected, and a single young male deermouse 20-30 days old was placed in each of the 12 nest boxes located in half of each plot. The section of each plot which was selected to receive these aliens was the area in which the residence centers of most homing animals were located. The young alien males were placed in the nest boxes approximately two hours before reintroduction of the residents and were retained there until the following morning. Retention of the aliens in the nest boxes was achieved by putting a tiny collar on each animal and attaching a fine wire leader to each collar. The leader was then snapped on a wire loop in the cover of each nest box. All other techniques and procedures for this homing test were similar to those of the previously described test.

Data recorded. Following reintroduction of the resident populations, the location of each mouse was recorded during the next three days. In those experiments in which aliens occupied the home nest boxes of residents, the presence or absence of the residents in the alien occupied nest boxes and the condition of the aliens were recorded. As indicated previously, all aliens were removed from the plots on the morning following reintroduction of the residents.

Population Removal

On the third morning of the homing phase of each experiment, all experimental mice were taken from the nest boxes, killed with chloroform, weighed, and the adrenal glands removed and weighed. Laboratory control animals were likewise sacrificed, weighed and dissected within approximately 24 hours before or after the experimentals. In the case of pregnant females, the number of young, and the weight of the uterus plus young were recorded in addition to the other measurements. The adrenals were removed from each animal as soon as possible after its death. Cleaning of the adrenals preparatory to weighing was done with a scalpel using a dissection microscope at 20X magnification. The adrenal glands rested on a wet paper towel on the stage to prevent desiccation. Weights to the nearest .2 milligram were obtained on a Roller-Smith Precision Balance.

General Procedures

Measurement of Feeding Activity

Excess food was available at the feeding stations at all times during each experiment. The feeding activity recording mechanism of each feeding station was activated during the eight nights intervening between the two trapping periods of each period of population establishment. These data will not be discussed here.

Observations

The nocturnal activities of the mice were observed with a flashlight or with the seven flood lights in the field.

Most observations were made immediately after release of the mice from the traps at two hours after sunset and while alien mice were on tethers near the feeding stations or in the vicinity of nest boxes known to be occupied by resident mice.

Alien mice were used to promote social interaction and were removed from the field immediately at the close of the observation period. The aliens wore a collar made of small fishing tackle snaps. A fine six inch wire leader was attached to a swivel on the collar and then to a stake in the ground (Figure 11). Since there were swivels at both ends of the leader, each mouse was free to move within a circular area of radius equal to the length of the leader. This confinement did not appear to impede the mice from moving and manipulating their bodies. In addition, the collars were apparently not detrimental to the mice since they wore them in the laboratory for several months with no ill effects.

Weather Recording

Weather data were recorded when possible at 8:00 A.M. each day. Data recorded included maximum and minimum temperatures, wet and dry bulb thermometer temperatures, and observational data on cloud cover and wind conditions. Also, a 24 hour thermograph recorded temperatures in the weather station in the field.

Air pressures were indicated on a "Taylor Cyclo-Stormograph" barometer which was located approximately 150 yards from the experimental field. A Taylor thermograph recorded outside temperatures at the same distance from the field.

Fig. 11. Tethering of alien mice for observational studies.

Additional weather information was obtained at an Official U. S. Weather Bureau Station at Acadia National Park, a distance of eight miles from the experimental area.

Predation Control

A steel trap was continuously set near each of five feeding stations to insure against predation by mammals. Predation was not an important factor in this research; for only seven out of 128 experimental animals disappeared during the periods of population establishment.

Recapitulation

Eight successive populations of Prairie Deermice were raised from weaning (21 days) in two social situations, either in isolation or in groups. The groups were composed of two mated pairs living on either side of a wire screen partition dividing a standard mouse box into two compartments. At ten weeks of age, four bisexual pairs from each social treatment were systematically released into different one-half acre "mouse proof" plots. Each experimental population remained in the plots a total of three weeks. During this time the location of each animal was recorded daily. Seventeen days after release, all mice were removed from each plot and kept in isolation in the laboratory for 36 hours. Each was then reintroduced into its home plot at a point distant to its previously established home area and the location of each for the next three days was recorded. In the experiments following the establishment of homing as a phenomonon, alien mice were in one-half of the nest boxes during the first night of the homing test. At the conclusion of each three week period, all field experimentals and their laboratory controls were killed with chloroform, weighed, and the adrenals removed and also weighed. The laboratory controls were the same age as the experimentals but had continued in the original social arrangements in the laboratory rather than being released in the plots.

During each experimental period other dynamics of the population were measured by two periods of live trapping, each four nights in duration; recording time of feeding activity; and direct observation of social interaction between residents and aliens.

RESULTS

Descriptive Measurements

A prerequisite to meaningful analysis and interpretation of the data is an understanding of the adaptation of the populations to the experimental situation. The following descriptive measures were taken as a means of gaining this understanding.

Use of the nest boxes. For the eight experiments reported here, a total of 1909 occurrences of mice in nest boxes was recorded during the periods of population establishment. One population of 8 animals was in each of the plots of the experimental field during every experimental period. The period of population establishment for 5 of the 8 populations of each social treatment was 16 days instead of the originally planned 17 days. This occurred because a few mice avoided capture and could not be removed from the plots on the day scheduled. Further, 11 mice (5 isolates and 6 group raised) of the 128 released in the plots died (4) or disappeared (7) during the period of population establishment. Adjusting for these deviations in the design, a total of 2023 recordings of mice in nest boxes was possible during the experiments. Thus, the mice were found in nest boxes 94.9% of the times possible.

Table V lists the mean number of different nest boxes occupied per mouse during the period of population establishment and during the last 10 days prior to removal from the

TABLE V

AVERAGE NUMBER OF DIFFERENT NEST BOXES OCCUPIED PER MOUSE* DURING THE PERIOD OF POPULATION ESTABLISHMENT

	Experiment	1	2	3	4	5	6	7	8	$\bar{X}$
Isolation Raised	Period of Establishment									
	Female	7.3	5	6	6	4.8	4.5	6	8.7	6.0
	Male	8.3	5.8	6.5	4.5	4.3	6	9.7	5.8	6.2
	Last 10 days									
	Female	5.8	2.3	4.7	4	3.5	4	4.8	5	4.3
	Male	6.7	4	4.5	2.8	3.5	4.3	4.8	4.5	4.4
Group Raised	Period of Establishment									
	Female	5	4.5	8.3	7	5.5	5.3	5.5	4.3	5.7
	Male	7	5.8	5.3	6.5	5	7.8	6.5	6.5	6.3
	Last 10 days									
	Female	4	3.3	6	5.5	4.3	4	4.3	2.3	4.2
	Male	4.3	3.5	5	4.5	3.7	4.8	4.3	4.5	4.3

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* Only data included from mice living in the plots 9 or more days after introduction.

field for the homing test. During the total period of population establishment, the isolation raised females and males were found in an average of 6.0 and 6.2 nest boxes respectively, while the group raised females and males were found in 5.7 and 6.3 nest boxes each. In the last ten days of each period of establishment, isolation raised females were found in an average of 4.3 nest boxes while males were in 4.4. Group raised females were in 4.2 boxes and males were in 4.3 during the same period of time. These data indicate no significant differences between sexes or social treatments in the average number of nest boxes occupied during each of the periods of measurement.

Moves between nest boxes. A daily tabulation was made of the average number of moves made per mouse to nest boxes not occupied on the previous day and nest boxes in which the mouse in question had never previously been recorded. The first measure shows the rate of changing nest boxes on successive nights. It incorporates the second, which measures inversely localization of the individuals.

Figure 12 shows the results of these measurements and indicates that:

(a) After a short period (1-3 days) of sedentary behavior subsequent to release in the field, a rapidly increasing proportion of mice of both social treatments moved to different nest boxes each day until day 7 or 8 of the period of population establishment.

(b) After day 7 or 8, the proportion of animals of both social groups moving to different nest boxes became relatively constant, whereas the proportion moving to previously unvisited nest boxes became smaller with passage of

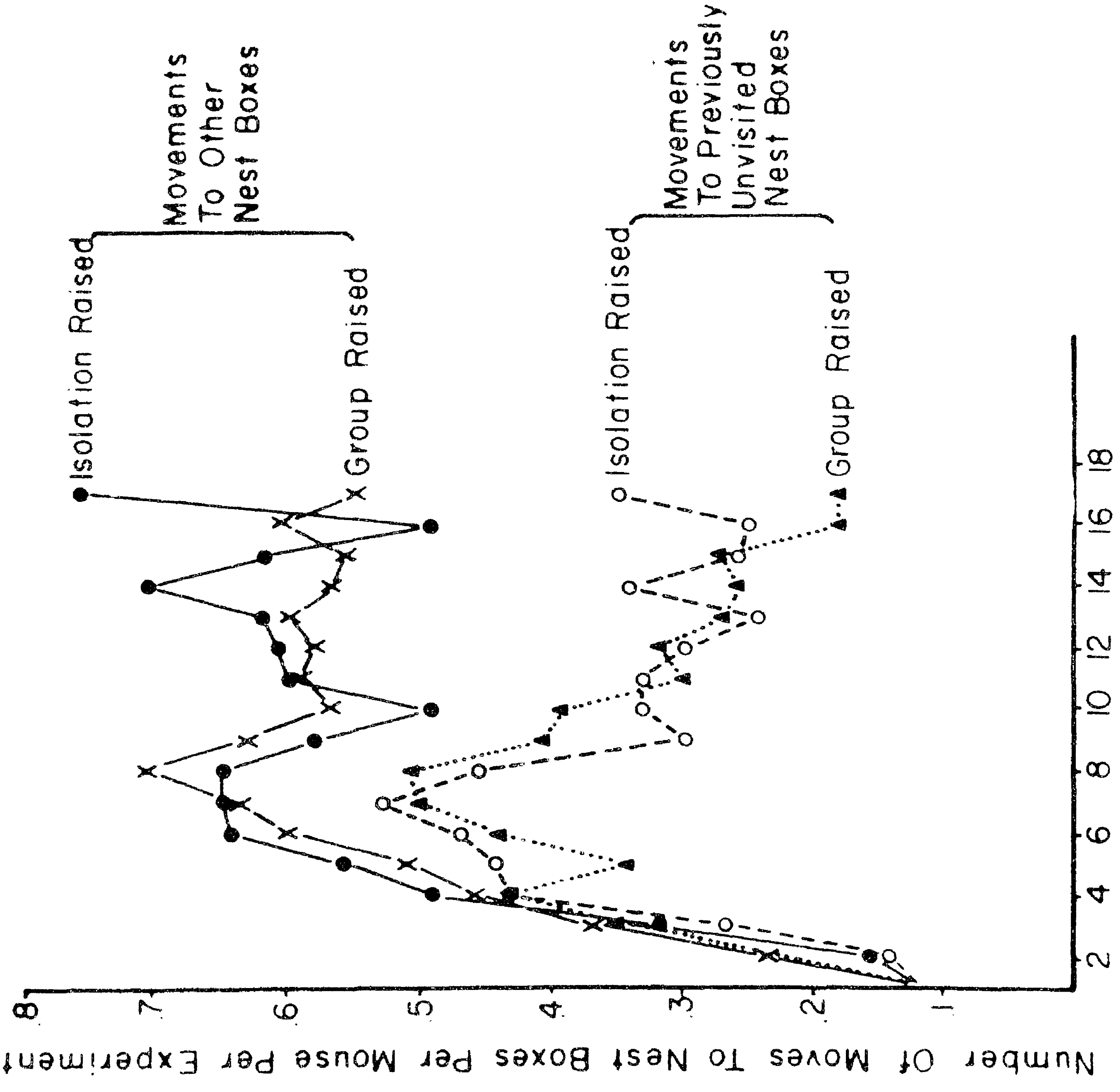

Fig. 12. Movements to previously unvisited nest boxes and to other nest boxes.

time. This downward trend of the curve measuring movements to strange nest boxes is not due to a decreasing availability of such nest boxes. Table V indicates that an average of only 6 nest boxes per mouse was occupied in the total period of population establishment.

(c) For both social treatments there was a highly significant difference, as indicated by the t test, between the average daily number of moves to strange nest boxes and moves to boxes not occupied the previous day ($P < .001$). Thus, mice of both social treatments continued to move to other nest boxes at a relatively steady rate, but their movements were to a few previously visited boxes.

(d) There was no significant difference between the two social treatments for either of these measures of movement.

<u>Distance moved between nest boxes</u>. The daily distance moved per mouse to different nest boxes and to boxes in which each mouse had never previously been recorded was measured for each population of the two social treatments. These data revealed:

(a) The same pattern of rapid increase in distance moved per mouse until day 7 for isolates and day 8 for group raised as shown in the preceding measurements of the number of moves per mouse.

(b) Following day 7 for the isolation raised mice and day 8 for the group raised animals, the curves of distance moved diverged similarly to the curves showing the number of moves (Figure 12). The proportion of the population moving to different nest boxes each day became relatively constant. The curve reflecting distance moved to strange nest boxes gradually sloped to lower values following the peak day. The only difference between the curves showing the number of moves (Figure 12) and those showing the distance moved was that the latter exhibited wider daily fluctuations.

(c) There was a highly significant difference within social treatments between the two distance measurements of movement. Significantly longer moves were made to different nest boxes than to strange boxes for each day ($P < .001$).

(d) There was no significant difference between group and isolation raised mice for either of the measures of distance moved.

Social Relationships

Gregarious behavior. Figure 13 shows the occurrence of mice along, in pairs, or in groups of three subsequent to release in the field. It may be seen that the mice of both social treatments were most often found alone and rarely combined in anything but bisexual pairs.

A three way analysis of variance of the gregarious behavior is shown in Table VI. Since some mice died during the experiments and others were not found in nest boxes consistently, the proportion of nest box records for each mouse in which it was alone was used as the unit of measurement.

A significantly higher proportion of the nest box records of isolation raised than of group raised mice was made while the animals were alone in the nest boxes. An F value of 4.48 with 96 degrees of freedom was significant at the 5% level. It follows that a higher proportion of nest box records of group raised than isolation raised mice were made while the mice were in combinations.

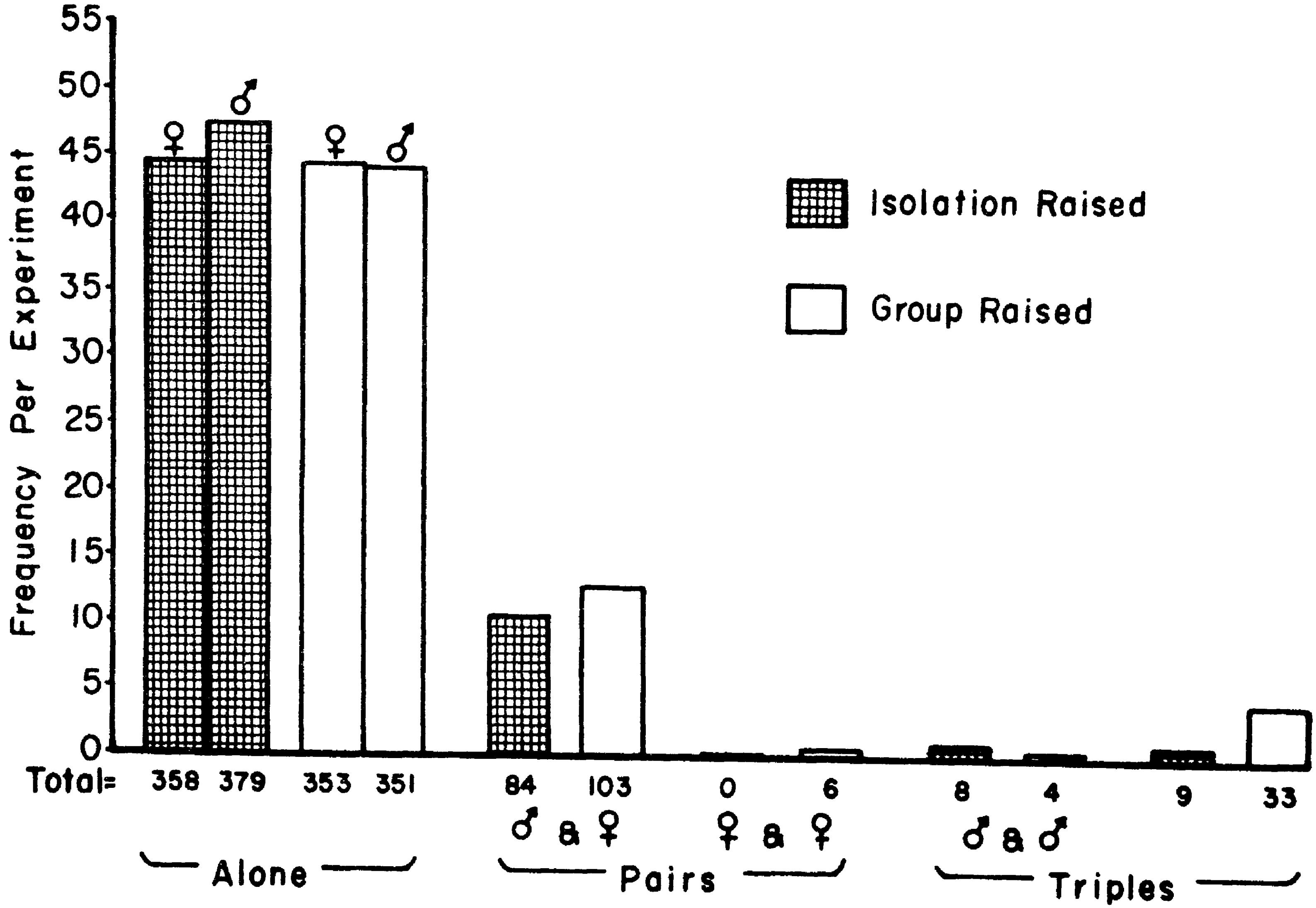

Fig. 13. Occurrence of mice alone, in pairs and in groups of three.

TABLE VI

ANALYSIS OF VARIANCE OF THE PROPORTION OF NEST BOX RECORDS IN WHICH MICE WERE ALONE

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Value
Total	127	61,978.49		
Between Experiments	7	5,511.80	787.4.	1.56
Between Social Treatments	1	2,269.69	2,269.69	4.48*
Between Sexes	1	79.69	79.69	.16
Social Treatment x Experiment	7	3,914.12	559.16	1.1
Social Treatment x Sex	1	7.51	7.51	.01
Sex x Experiment	7	962.62	137.52	.27
Sex x Experiment x Social Treatment	7	647.81	92.54	.18
Error	96	48,585.25	506.10	

* Significant at 5% level.

It is of further interest to note that no combinations of isolation raised animals other than bisexual pairs occurred before the last experiment (October 31 to November 21). Group raised mice were found in combinations other than bisexual pairs prior to this time, although males were never found together until this last experiment. It is possible that cooler temperatures or some other environmental factor were responsible for this change in behavior.

Pair combinations. Chi-square tests (Table VII) of the significance of the observed frequency of bisexual or monosexual pairs indicate that all pair combinations occurred in different frequencies than expected by chance. Bisexual pairs occurred significantly more often and monosexual pairs significantly less often than expected.

TABLE VII

COMPARISON OF OBSERVED FREQUENCIES OF PAIRS WITH THAT EXPECTED BY CHANCE

	Isolation Raised		Group Raised	
	Observed	Expected	Observed	Expected
2 males	4	22	2	27
2 females	0	22	3	27
1 male and 1 female	84	44	103	54
Chi Square	73.1***		88.9***	

*** = Level of Significance = $P < .001$

Monosexual combinations. A test of differences in frequencies of combining with the same sex was made for each social treatment. The data are presented in Table VIII.

TABLE VIII

RECORDS OF MICE IN NEST BOXES WITH THE SAME SEX OR OTHERWISE

	Isolation Raised		Group Raised	
	With Same Sex	Other Records	With Same Sex	Other Records
Females	0	445	18	473
Males	14	469	14	470

A Chi-square test between sexes for each social treatment revealed a highly significant difference ($P < .001$) between sexes for the isolation raised mice and no difference between the group raised animals. The isolation raised males combined significantly more frequently with other males than the females did with other females.

Comparison of the two social treatments revealed no significant differences between males in the proportion of nest box records in which they were found with at least one male. The group raised females, however, were combined with females a higher proportion of times than isolation raised females ($P < .001$).

Bisexual combinations. All instances in which at least 2 mice of opposite sex occurred together in a nest box are the basis for the following discussion. The important measurements of bisexual combination are given in Table IX.

TABLE IX

BISEXUAL COMBINATIONS*

Category	Isolation Raised Female	 Male	Group Raised Female	 Male
Number of mice in population (N)	30	30	32	30
Number of mice found with a mouse of the opposite sex (O)	22	18	27	24
Number of different bisexual combinations (#)	27	27	38	38
Number of days in bisexual association (#)	90	90	125	125

* Mice must have been present in the plots on the 9th day after introduction to be included in this table.
(#. N. O) = Symbols used in Figure 15.

Figure 14 shows the proportion of each sex found with the opposite sex at least once and the average number of days spent in each bisexual combination. There were no significant differences between social treatments with regard to these measurements, although, the proportion of mice combining with the opposite sex was larger for the group raised mice than for isolation raised mice ($.1 > P \geq .05$).

Figure 15 illustrates the number of bisexual combinations and the total number of days mice of each social treatment were found in a bisexual combination of any type. The number of events (# in Table IX) in each category was adjusted by dividing by (N), the total number of animals of the sex being measured or by (O), the number of mice which combined in bisexual combinations. This second method removed the effect of differential rates of combination and compared the two sexes and the social treatments on the basis of the number of animals which were found with the opposite sex. The analyses of the differences between social groups are discussed below.

Different bisexual combinations. Comparisons of these data were made with the t test and although no differences were significant at the 5% confidence level, there were several which showed a consistent low level of probability of occurrence by chance. These comparisons and the P value for each are listed in Table X.

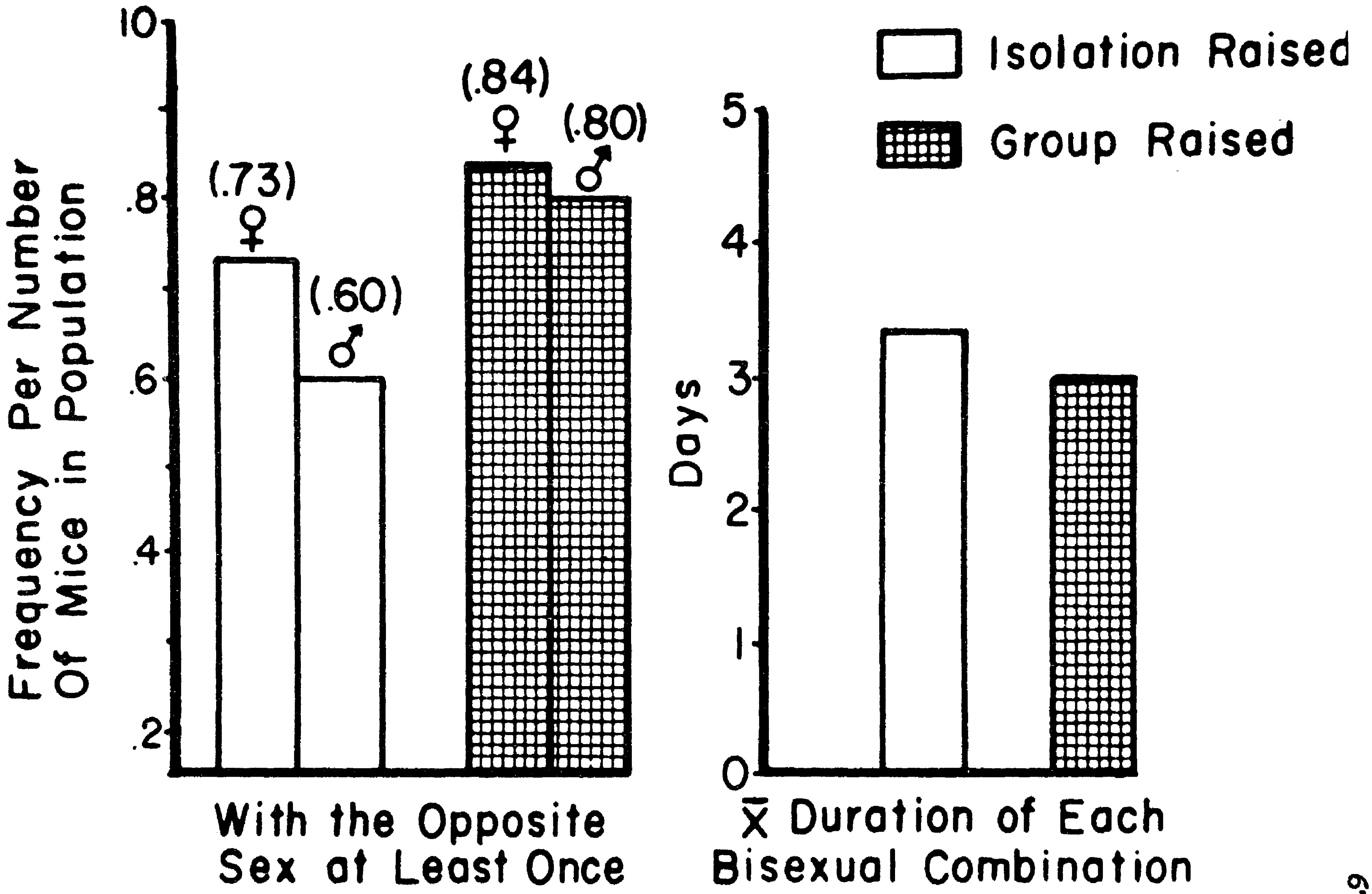

Fig. 14. Proportion of mice found with the opposite sex and the mean duration of each bisexual combination.

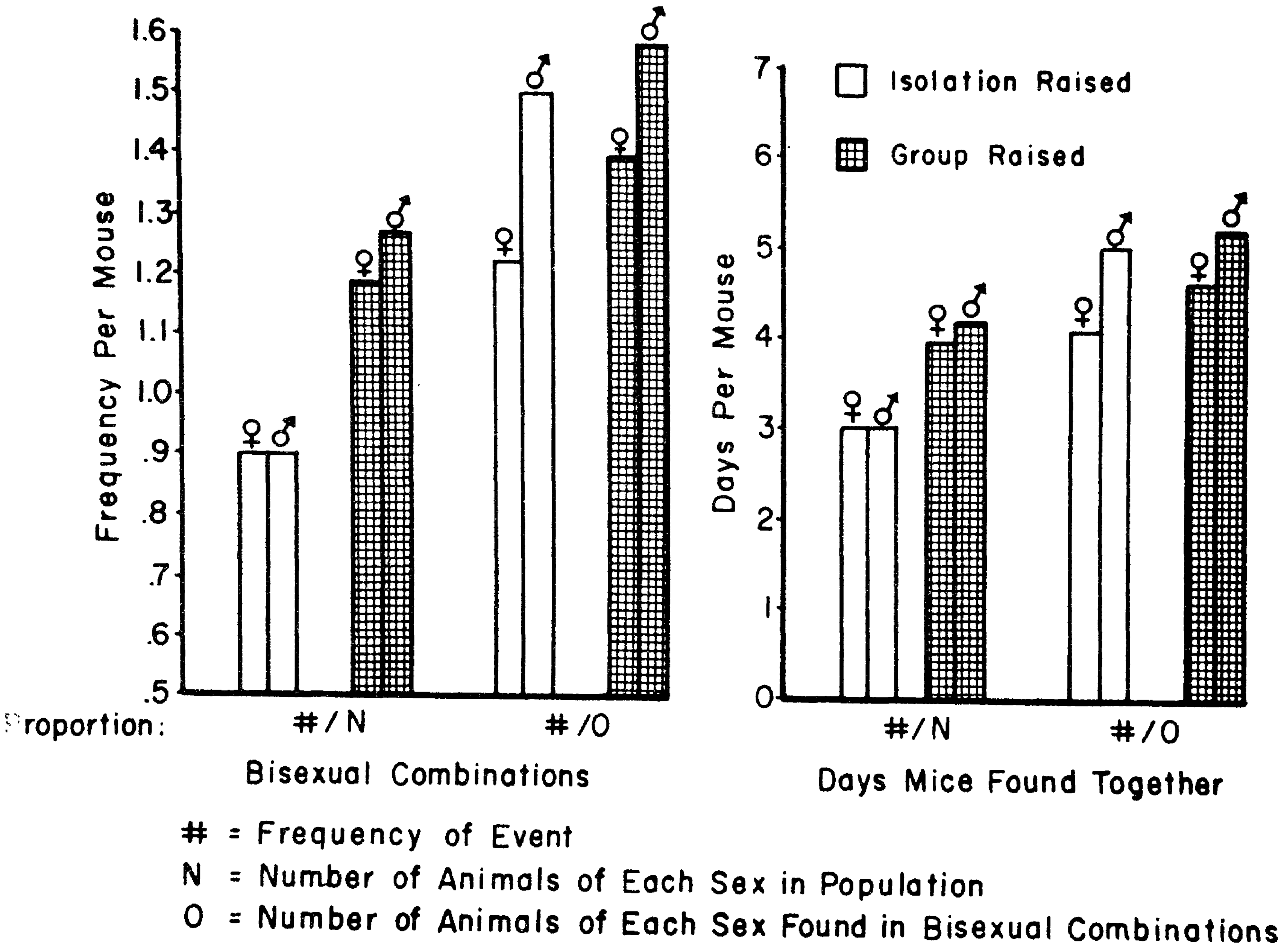

Fig. 15. The number of different bisexual combinations and days in combinations.

TABLE X

COMPARISON OF NUMBERS OF BISEXUAL COMBINATIONS

Comparison	Larger Number of Combinations	Significance Level #/N	Significance Level #/O
Isolation vs. Group			
All mice	G > I	$(.2 > P > .1)$	$(.5 > P > .4)$
Females	G > I	$(.3 > P > .2)$	$(.4 > P > .3)$
Males	G > I	$(.2 > P > .1)$	$(P > .5)$
Males vs. Females			
Group raised	♂ > ♀		$(.4 > P > .3)$
Isolation raised	♂ > ♀		$(.2 > P > .1)$
All mice	♂ > ♀		$(.05 > P > .02)$

# = Frequency of event.
N = Number of animals in population.
O = Number of animals combining with the opposite sex.
G = Group raised mice.
I = Isolation raised mice.

Group raised animals occurred in consistently, but not significantly, higher numbers of bisexual combinations than the isolation raised mice. Further, males of both social treatments combined with more females than females did with males. When data for like sexes from both social groups were combined, males were found in a significantly greater number of bisexual combinations than females $(.05 > P > .02)$.

Duration of bisexual combinations. Differences between social treatments in the total number of days mice were found in bisexual combinations (Figure 15) were measured by t tests. Group raised mice were in combinations (#/N) a longer period of time than isolates, although, not at the

$P = .05$ level of significance (Table XI). No differences between the two sexes of each social treatment were evident from these analyses.

TABLE XI

COMPARISON OF THE DURATION OF BISEXUAL COMBINATIONS

Comparison	Larger Number of Days	Significance Level #/N	Significance Level #/O
Isolation vs. Group			
All mice	G > I	$(.3 > P > .2)$	$(P > .5)$
Females	G > I	$(.3 > P > .2)$	$(P > .5)$
Males	G > I	$(.3 > P > .2)$	$(P > .5)$
Males vs. Females			
Group raised	♂ > ♀		$(P > .5)$
Isolation raised	♂ > ♀		$(.5 > P > .4)$
All mice	♂ > ♀		$(.02 > P > .01)$

\# = Frequency of event.
N = Number of animals in populations.
O = Number of animals combining.
G = Group raised mice.
I = Isolation raised mice.

When the results concerning the total number of animals of the same sex were combined and then compared, males were found to have been in bisexual combinations (#/O) a significantly greater number of days than were females $(.02 > P > .01)$.

The influence of the social treatments upon bisexual combinations may be summarized by saying that a higher proportion of group raised mice combined; they formed a greater number of different combinations; and they continued in combinations for a longer period of time than isolation raised mice. Consistent differences between isolation raised and group raised mouse populations have not been demonstrated to be statistically significant by individual test comparisons. A significant difference between the social treatments has been shown, however, by the 3-way analysis of variance shown in Table VI. There, the units of measurement were the proportion of nest box recordings in which mice were either alone or combined with other mice. In that analysis, group raised mice were in combinations for a significantly higher proportion of nest box records than isolates.

Latency of combining with the opposite sex. The number of days that elapsed following introduction to the field before each mouse was found with a mouse of the opposite sex was recorded. The percentage of mice of each social treatment found for the first time with an animal of the opposite sex for each day is indicated (Figure 16) as an accumulative percentage curve. The distributions for the social treatments were compared by the Kalmogorov-Smirnov test and group raised mice were found to combine with the opposite sex significantly sooner ($P < .001$) after introduction to the field than the isolation raised mice.

No comparison was made of the latency of combining with the same sex because of the low frequency of such events.

Establishment and termination of bisexual pairs. Mice were not recorded as bisexual pairs unless they were found together in a nest box at the time of the daily check.

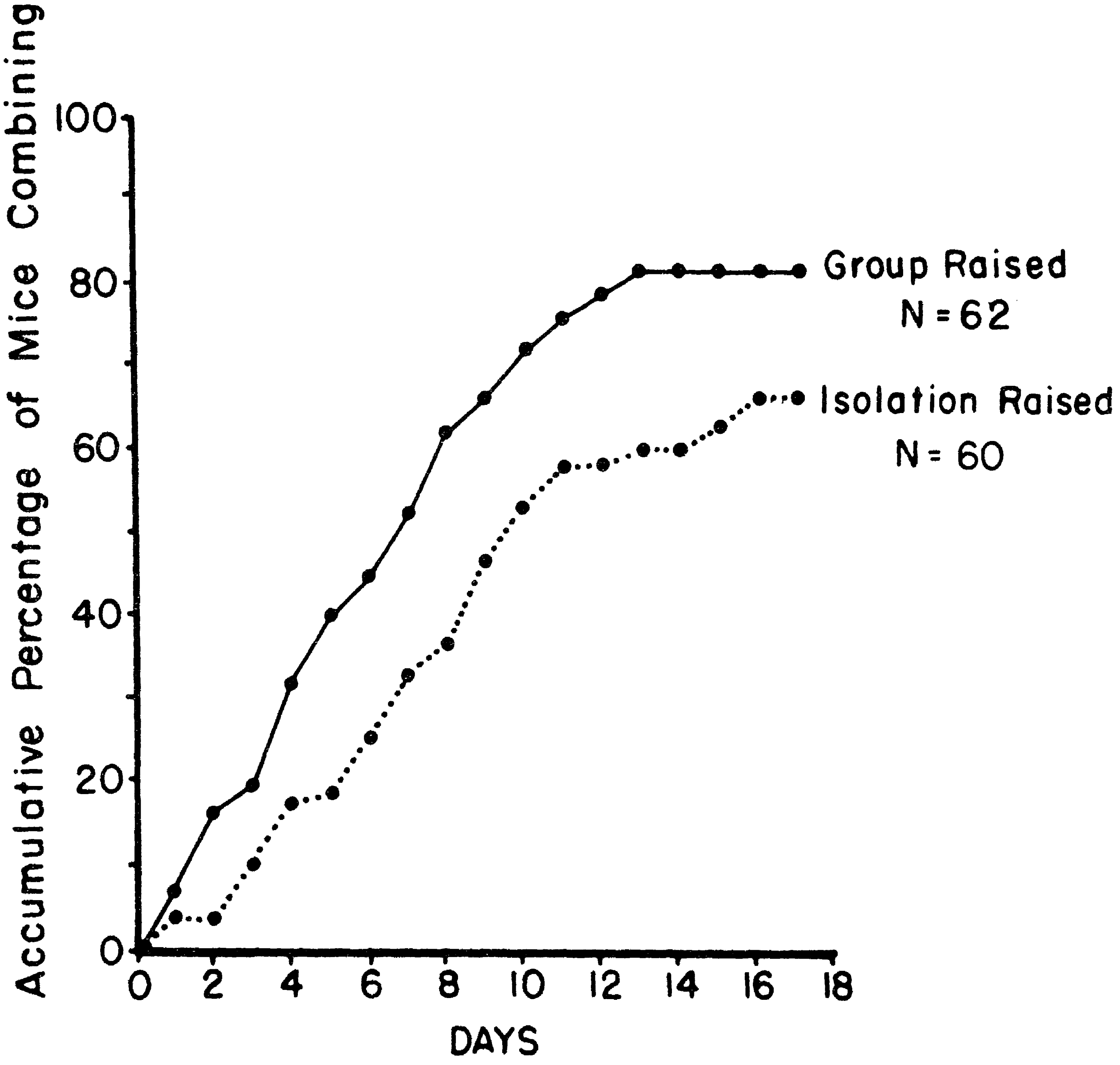

Fig. 16. Latency of combining with the opposite sex.

These data, therefore, offer a means by which sex differences in originating bisexual pairs may be inferred.

On the first day of each period of association, the location of the mice was recorded. Occurrence of each pair in a nest box occupied the previous day by the male or by the female was noted. Mice which moved into nest boxes occupied the previous day by the mouse of the opposite sex were regarded as originating the bisexual pair. These data are tabulated in Table XII.

TABLE XII

ORIGINATOR AND TERMINATOR OF BISEXUAL PAIRS

	Isolation Raised		Group Raised	
	Male	Female	Male	Female
Animal forming pair	14	10	17	20
Animal leaving first	15	6	15	13

Table XII also contains a tabulation of the first animal leaving the bisexual pair. The totals of animals forming and leaving pairs are not the same because some mice were still in pairs when the experiments ended. Other pairs were enlarged to groups of three. Tests failed to show significant differences between social treatments for each of these measurements. No significant differences were found between sexes as to which animal originated or terminated the bisexual pair.

Successive occupancy of nest boxes. As a further means of evaluating the individual responsibility for originating bisexual pairs, a tabulation (Table XIII) was made of the replacement of one mouse by another. The sex of the mouse moving into the nest box and that of the mouse which had been in the nest box the preceding day was recorded. Records were made only when the animal moving out had not been living on the previous day with the one which replaced it.

TABLE XIII

FREQUENCY AND SEX OF MICE OCCUPYING NEST BOXES ON SUCCESSIVE DAYS

	Isolation Raised		Group Raised	
Succeed:	Male	Female	Male	Female
Male	6	12	3	15
Female	23	3	31	7

There was no significant difference between social treatments with regard to these measurements. The frequencies with which each sex succeeded the opposite or the same sex were significantly different ($P < .001$). Animals of one sex were succeeded in nest boxes by mice of the opposite sex significantly more often than by mice of the same sex. A comparison of the frequencies with which animals of the opposite sex succeeded each other and those expected by chance indicated that females succeeded males a significantly greater number of times than expected while males succeeded females significantly less than expected. Conversely, animals of the same sex did not succeed each other at a different frequency than expected by chance.

These differential rates of nest box succession may be a result of: attraction between mice of the opposite sex so that they succeed each other because one sex was in the nest box the previous day; avoidance of animals of the opposite sex. Succession is due to movement by a mouse away from a nest box because of invasion by a mouse of the opposite sex.

The low frequencies of moves into nest boxes occupied previously by like sex mice may be indicative of a repulsion between like sex animals. This may operate to keep mice of the same sex in separate spatial areas.

A further insight may be had by combining the data measuring the originator and terminator of bisexual pairs with the succession data discussed above. If these data are grouped assuming a tendency to leave or avoid combinations, the following summation may be made:

		Males	Females
Leave	Left nest boxes invaded by the opposite sex.	54	27
Stay	Remained in the nest box when the opposite sex came in.	30	31

A significant difference was not shown (Chi-square) between males and females with regard to leaving or remaining in a nest box when a mouse of the opposite sex moved in. A P value of .06 indicates the tendency for males to leave more and remain less than females when a mouse of the opposite sex moves in. It should be remembered, however, that this analysis was made with the assumption that the mice left the nest boxes because an animal of the opposite sex moved into the box. The reverse may be true, that is, the immigrant animal may have moved in because the other mouse had been there.

Observations. Direct observations were made in the field to evaluate the type and extent of territorial behavior. In general these data were collected in two ways. Observations were made of interactions between animals following their release from live traps in the field. Mice could be seen and followed as they approached other mice or traps. A headlight was used for these observations and, provided the observer moved slowly, there was no noticeable affect upon the behavior of the mice.

Other observations were made at nest boxes known to be occupied by residents. Alien mice were tethered outside of these occupied nest boxes and social interactions were observed when the residents left the boxes. The observations were grouped in the following manner and the frequency of each is given: attacks (8): one mouse either attacked or directly charged the other mouse causing it to run away, submit, or assume a defensive posture (Agonistic Behavior, Scott, 1956); avoidance (15): both animals saw each other and moved away from each other; ignoring (2): both animals saw each other but no detectable repulsion or avoidance behavior took place.

Of the 5 attacks made upon aliens tethered outside resident nest boxes, 2 were made by one female against 2 different aliens and 2 by 1 male against the same alien on successive nights. All attacks were of short duration and were terminated by the resident leaving the area. The attacks seemed designed to drive the aliens away, but since the aliens were tethered, this was impossible and resulted in the residents leaving instead. These relatively few data indicated that avoidance, or bluffing may be a method of apportioning the area among the animals of a population.

Spatial Patterns

Spatial distribution was measured as the distance to the nearest neighbor (Clark and Evans, 1954, 1955). The following categories of nearest neighbor measurements were taken, the means of which are listed in Table XIV.

Distance to:

Nearest neighbor of the same sex.
Nearest neighbor of the opposite sex.
Nearest neighbor of either sex.

TABLE XIV

AVERAGE DISTANCE TO NEAREST NEIGHBOR*

	Isolation Raised		Group Raised	
From:	Males	Females	Males	Females
To mice of:				
Same sex	56.9	65.18	58.4	62.3
Opposite sex	38.49	38.18	34.82	33.73
Either sex	30.64	34.48	30.32	28.98

* Distance measured in feet.

In all but one distance measurement taken, isolation raised mice were more widely separated than group raised mice. The only exception was that group raised males were dispersed a greater average distance than isolation raised.

Statistical comparisons between isolate and group mice of the same sex were made for the daily distance measurements in the 3 categories outlined above. The results of these analyses are shown in Table XV.

TABLE XV

COMPARISONS OF THE AVERAGE DAILY DISTANCE TO THE NEAREST NEIGHBOR DURING THE PERIOD OF POPULATION ESTABLISHMENT

Comparison	Significance Of Greater Distance To: Same Sex	Opposite Sex	Either Sex
Isolation vs. Group			
Females	$I > G$ $(.05 > P > .02)$	$I > G$ $(.02 > P > .01)$	$I > G$ $(P < .001)$
Males	$G > I$ $(.1 > P > .05)$	$I > G$ $(.05 > P > .02)$	$I > G$ $(P > .5)$
Males vs. Females			
Group Raised	♀ > ♂ $(.3 > P > .2)$	♂ > ♀ $(.3 > P > .2)$	♂ > ♀ $(.3 > P > .2)$
Isolation Raised	♀ > ♂ $(.02 > P > .01)$	♂ > ♀ $(P > .5)$	♀ > ♂ $(P < .001)$

I = Isolation raised mice.
G = Group raised mice.

There were no significant differences between isolation raised and group raised females and between isolation raised and group raised males in the distance to the nearest neighbor of the same sex when compared for the total period of establishment. Only five populations of each social treatment had a 17 day period of population establishment. Thus, a radical difference in the distance to the nearest neighbor on day 17 for one experiment could greatly affect the average for all experiments. This happened in the measurement of distance to nearest neighbor of the same sex. Therefore, the social treatments were compared using only data from the first 16 days. Isolation raised females were significantly further from other females than group raised females $(.05 > P > .02)$. Conversely, group raised males were further from other males in the populations than isolation raised males $(.1 > P > .05)$.

The average daily distance to animals of the opposite sex was significantly greater for isolation raised females $(.02 > P > .01)$ and males $(.05 > P > .02)$ than their group raised counterparts.

Comparison of the distance to nearest neighbors of either sex showed that isolation raised females were significantly more dispersed than group raised females $(P < .001)$ while isolate males did not differ from group males $(P > .5)$.

When the sexes were compared within social treatments, isolation raised females were found at greater distances from females than males were from males $(.02 > P > .01)$. This was not statistically demonstrated for group raised females $(.3 > P > .2)$. There was no significant difference for either social treatment in the distance to nearest neighbor of the opposite sex. Isolation raised females were significantly further away than males from animals of either sex $(P < .001)$. Among group raised mice, males were further away than females although not significantly so $(.3 > P > .2)$.

The above analyses indicate that isolation raised females maintained a greater distance to nearest neighbors than group raised females. Males were not as consistent as females, however. The only significant difference found when comparing males showed isolate males further away from females than group raised males. Group males occurred further away from other males than isolate males, although not significantly so. These differences in male and female behavior may be indicative of a differential affect of the social treatments upon the two sexes.

Homing

Establishment of the homing phenomenon. Homing was established as a phenomenon in a series of 9 experiments involving 4 populations of isolation raised mice and 5 populations of group raised mice. Following the 36 hour period in the laboratory, a total of 30 isolation raised and 35 group raised mice were reintroduced into the field. The results of these experiments will be discussed as combined data, incorporating material from both social treatments, and separately with regard to each social treatment.

Figure 17 shows the percentage of mice homing by the first and third day after reintroduction to the field. Out of 65 animals released, 45 homed by day 1 and 52 by day 3. Since each mouse occupied an average of 4.3 nest boxes during the last 10 days preceding removal from the field for the homing test (Table V), a homing success required a rigorous discrimination of nest boxes.

The homing behavior of populations of isolation raised and group raised mice is shown in Figure 18. Thirty isola-

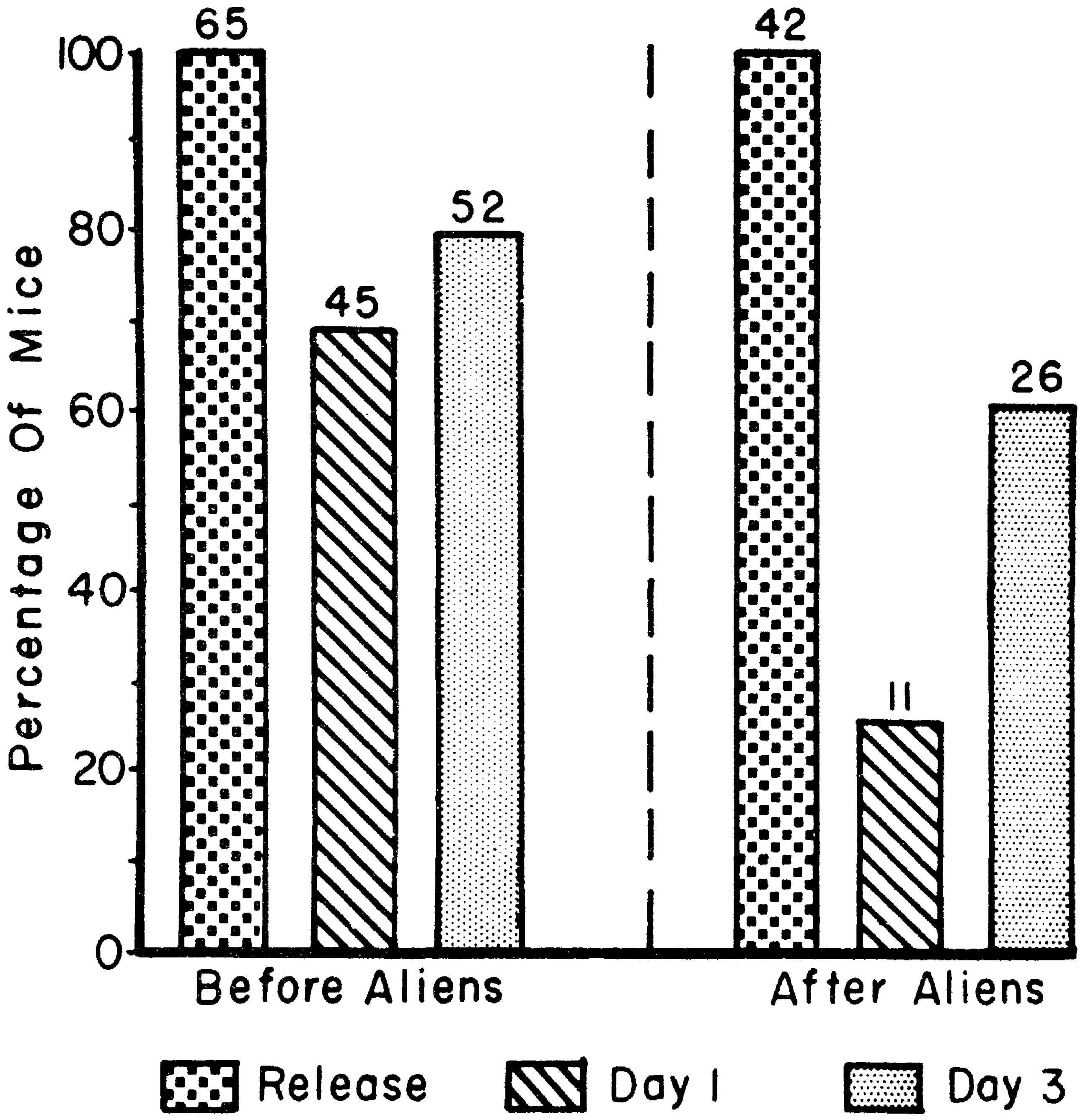

Fig. 17. Percentage of mice homing before and after aliens - combined data.

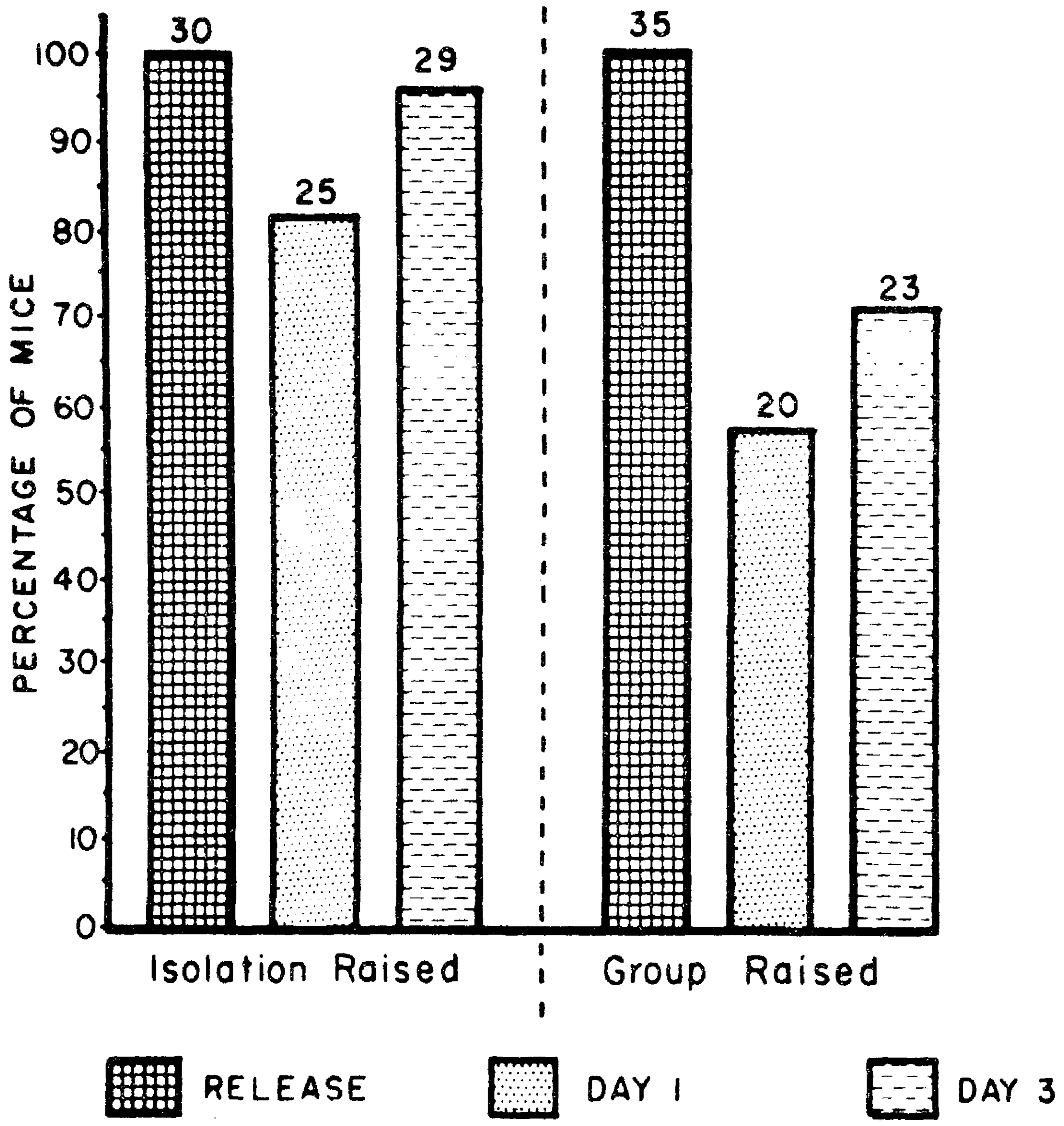

Fig. 18. Percentage of mice homing before aliens - social treatments.

tion raised mice were reintroduced to the field, of which 25 homed by day 1 and 29 by day 3. Twenty of the 35 group raised mice homed by day 1 and 23 by day 3.

Significance tests were made comparing the observed homing behavior of the mice with that which would be expected by chance if there were no homing. The comparisons made for the combined data as well as for the social treatments and the levels of significance calculated are indicated in Table XVI. It may be seen that homing in all categories was greater than expected by chance.

TABLE XVI

HOMING BEHAVIOR IN EXPERIMENTS PRIOR TO ALIEN INTRODUCTION

Comparison	Larger Frequency and Significance	
	Day 1	Day 3
Observed homing vs. that expected by chance		
Combined data	$O > E$ $(P < .001)$	
Isolation raised	$O > E$ $(P < .001)$	
Group raised	$O > E$ $(.01 > P > .001)$	
Isolation Raised vs. Group Raised	$I > G$ $(.05 > P > .02)$	$I > G$ $(.01 > P > .001)$

O = Homing observed.
E = Homing expected.
I = Isolation raised mice.
G = Group raised mice.

A comparison of the homing performance of the mice of the two social treatments (Table XVI) showed that a significantly higher proportion of isolation raised than group raised mice homed on both day 1 ($P < .05$) and day 3 ($P < .01$).

Homing with aliens temporarily in the field. As mentioned in the procedures, the homing phase of experiments 6, 7, and 8 differed from those of the preceding experiments in which homing was established as a phenomenon. During the later experiments, young male aliens were retained in one-half the nest boxes during the first night following reintroduction of the residents.

Figure 17 shows the combined homing performance for all mice released during these experiments. Of the 42 mice released, 11 homed by day 1 and 26 by day 3.

With regard to the social treatments, a total of 19 isolation raised mice were released while aliens were in the plots, of which 5 homed by day 1 and 13 by day 3. Of the 23 group raised mice reintroduced to the plots, 6 homed by day 1 and 13 by day 3.

Table XVII shows the results of tests comparing the homing performance before and after aliens were temporarily in the plots. Exact probabilities were calculated in those comparisons in which expected values less than 5 occurred.

On day 1, homing performance was significantly poorer than that recorded in establishing the homing phenomenon. Thus, introduction of aliens for one night significantly reduced the homing performance on that night.

TABLE XVII

COMPARISONS OF HOMING PERFORMANCE BEFORE AND AFTER ALIEN INTRODUCTION

Comparison	Larger Frequency and Significance	
	Day 1	Day 3
Comparing homing before and after aliens		
Combined data	$B > A$ $(P < .001)$	$B > A$ $(.1 > P > .05)$
Isolation raised	$B > A$ $(P < .001)$	$B > A$ $(P = .0116)$
Group raised	$B > A$ $(.05 > P > .02)$	ND $(P > .5)$

A = Homing with aliens temporarily in field.
B = Homing rate when establishing homing as a phenomenon.
ND = Difference in frequencies small or none.

The presence of aliens significantly reduced the homing performance during the first night for both isolation raised and group raised mice. Homing performance by day 3 was significantly poorer than before aliens for isolation raised mice only.

Differential homing with aliens in the field. As indicated in the procedure, the plots were divided transversely and aliens were placed in the 12 nest boxes in one-half of each plot. Thus, only half the mice of each reintroduced population were homing to nest boxes into which aliens had been placed.

Figure 19 illustrates the combined homing behavior under these differential conditions. The performance of isolation raised and group raised mice is shown in Figure 20.

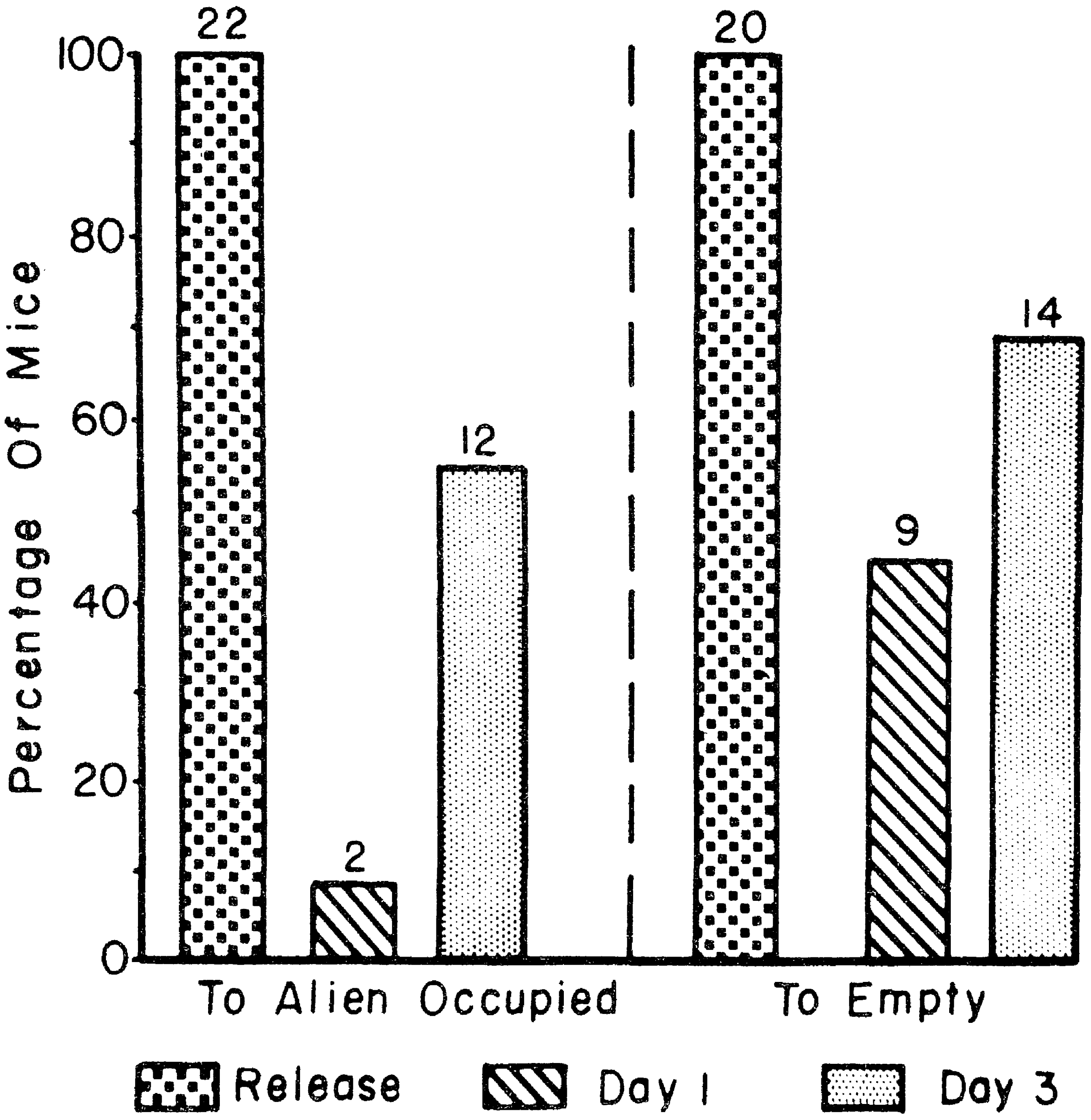

Fig. 19. Percentage of mice homing to alien occupied or to empty nest boxes - combined data.

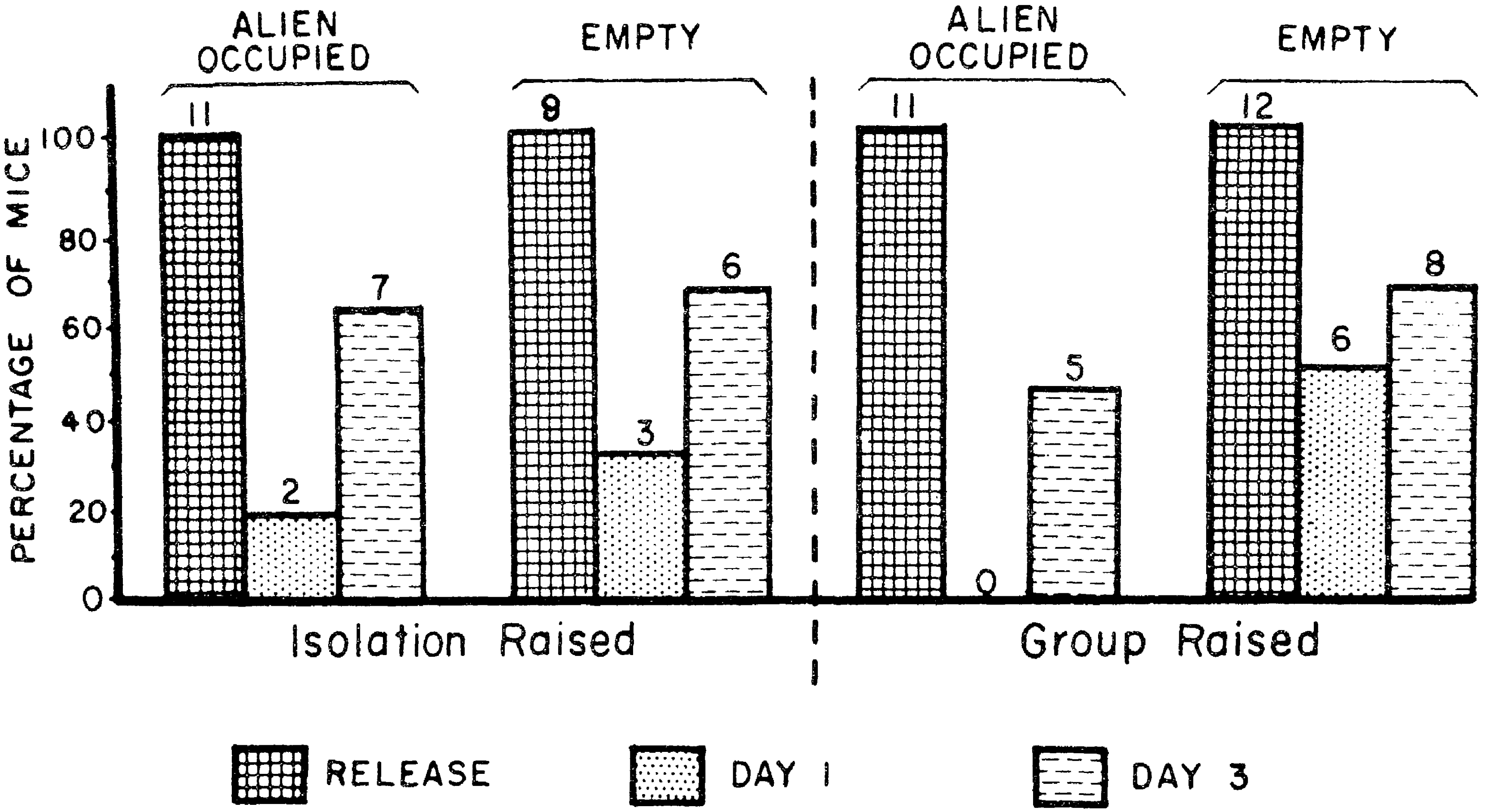

Fig. 20. Percentage of mice homing to alien occupied or to empty nest boxes - social treatments.

Table XVIII shows the results of statistical comparisons of homing to each type of nest situation with the performance prior to alien introduction.

TABLE XVIII

HOMING TO ALIEN OCCUPIED OR EMPTY NEST BOXES

Comparison	Larger Frequency and Significance	
	Day 1	Day 3
Homing after aliens compared with that before aliens		
To empty nest boxes		
Combined data	$B > A$ $(.1 > P > .05)$	ND
Isolation raised	$B > A$ $(.02 > P > .01)$	$B > A$ $(.05 > P > .02)$
Group raised	ND	ND
To occupied nest boxes		
Combined data	$B > A$ $(P < .001)$	$B > A$ $(.05 > P > .02)$
Isolation raised	$B > A$ $(P = .00007)$	$B > A$ $(P = .0136)$
Group raised	$B > A$ $(.01 > P > .001)$	$B > A$ $(.5 > P > .3)$

A = Homing with aliens temporarily in field.
B = Homing rate when establishing homing as a phenomenon.
ND = Difference in frequencies small or none.

When the data for both social treatments were combined, homing to empty nest boxes was not significantly different than that observed in populations before the aliens were placed in the field (Table XVI). Of the 20 mice released, 9 had homed to empty boxes by day 1 and 14 by day 3. Only 2 of the 22 mice released which were homing to occupied nest boxes did so by day 1 while 12 had homed by day 3. The homing success to occupied nest boxes was significantly less on both day 1 ($P < .001$) and on day 3 ($.05 > P > .02$).

Thus, while the combined homing rate to empty boxes was not different from the established rate on day 1 or 3, homing to alien occupied nest boxes was significantly less on both days.

Isolation raised mice homed significantly less after aliens than before aliens no matter whether they were returning to empty or occupied nest boxes. Of the 8 mice returning to empty nest boxes (Figure 20), only 3 homed by day 1 ($.02 > P > .01$) and 6 by day 3 ($.05 > P > .02$). Only 2 of the 11 mice homing to alien occupied nest boxes did so on day 1 ($P = .00007$) and 7 by day 3 ($P = .0136$). Thus, the presence of aliens in the field for the first night after reintroduction of the residents disrupted the homing performance of isolation raised mice returning to empty, as well as occupied, nest boxes. This was true on both day 1 and day 3.

Subsequent to alien introduction, group raised mice did not significantly differ in their homing to empty boxes from the rate observed prior to introduction of aliens. Of the 12 mice returning to empty nest boxes, 6 did so by day 1 and 8 by day 3. There were 11 group raised mice homing to occupied nest boxes. Of these none homed by day 1 and only 5 did so by day 3. Comparison of the proportion of homing successes observed with that in establishing homing as a phenomenon shows a significant difference on day 1 only ($.01 > P > .001$). The deleterious affects of introduction of aliens upon homing performance was evident only upon these mice homing to alien occupied nest boxes. This was true only for day 1 and did not have the longer lasting effects as observed for the isolation raised mice.

Differences in homing behavior following introduction of aliens were evident for both isolation raised mice and group raised mice when compared with homing performance established before aliens. Generally, isolation raised animals showed greater differences in homing following alien introduction than group raised mice.

Comparison of Social Treatments. Following alien introduction there were no significant differences between social treatments in homing per se, homing to empty nest boxes, or homing to occupied nest boxes.

Occurrence in Empty or in Alien Occupied Nest Boxes

Figure 21 shows the percentage of reintroduced residents which were found in nest boxes in which an alien had not been placed or in nest boxes in which aliens had been present. A total of 42 mice were reintroduced into the field as part of the homing tests. Of these 6 were found in occupied and 26 in empty nest boxes on day 1. By day 3 twenty mice had been recorded in alien occupied and 27 in empty nest boxes. The number of mice recorded for day 3 exceeded

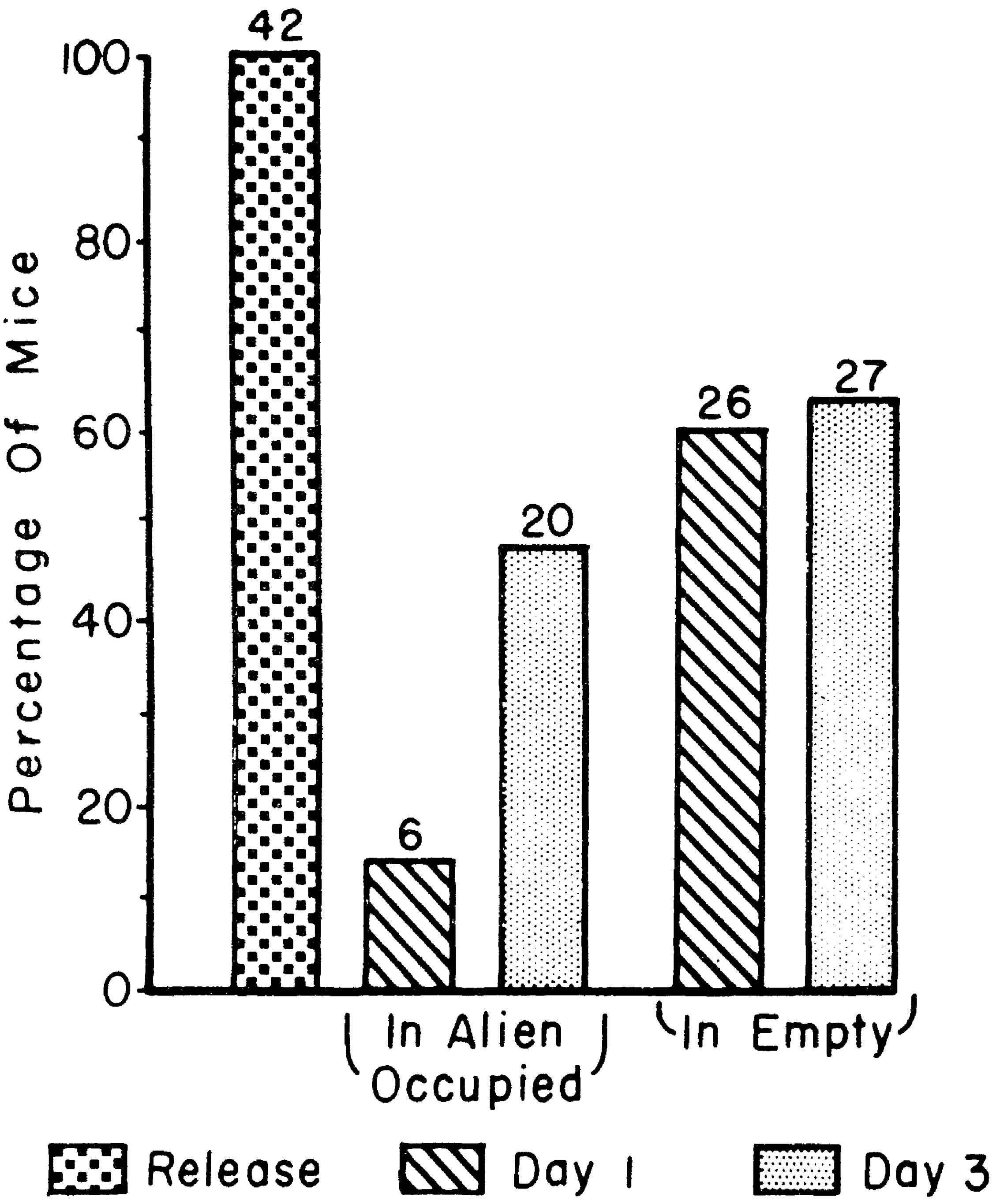

Fig. 21. Percentage of mice found in alien occupied or in empty nest boxes - combined data.

the number reintroduced to the field because some mice were recorded in more than one nest box during the 3 days subsequent to introduction.

There were no significant differences between social treatments in the number of mice found in empty or occupied nest boxes. The occurrence of mice in occupied or empty nest boxes is shown in Figure 22. Of the 19 isolation raised mice introduced to the plots, 2 were in occupied nest boxes and 10 in empty nest boxes on day 1. By day 3 ten mice had been in occupied nest boxes and 11 in empty boxes.

Twenty-three group raised mice were reintroduced to the field. Four of these were recorded in occupied nest boxes on day 1 and 16 in empty nest boxes. By day 3, ten had been in alien occupied boxes and 16 had been in empty boxes.

Since one-half of the nest boxes were empty and one-half were occupied by aliens, half of the mice could be expected to be in each type of nest box. Mice occurred in empty nest boxes significantly more often than expected by chance for both the combined data and for the populations of each social treatment.

Comparison of the total numbers of mice found in each of the two types of nest boxes revealed that a significantly higher proportion of the mice were found in empty boxes on day 1 than were found in occupied boxes.

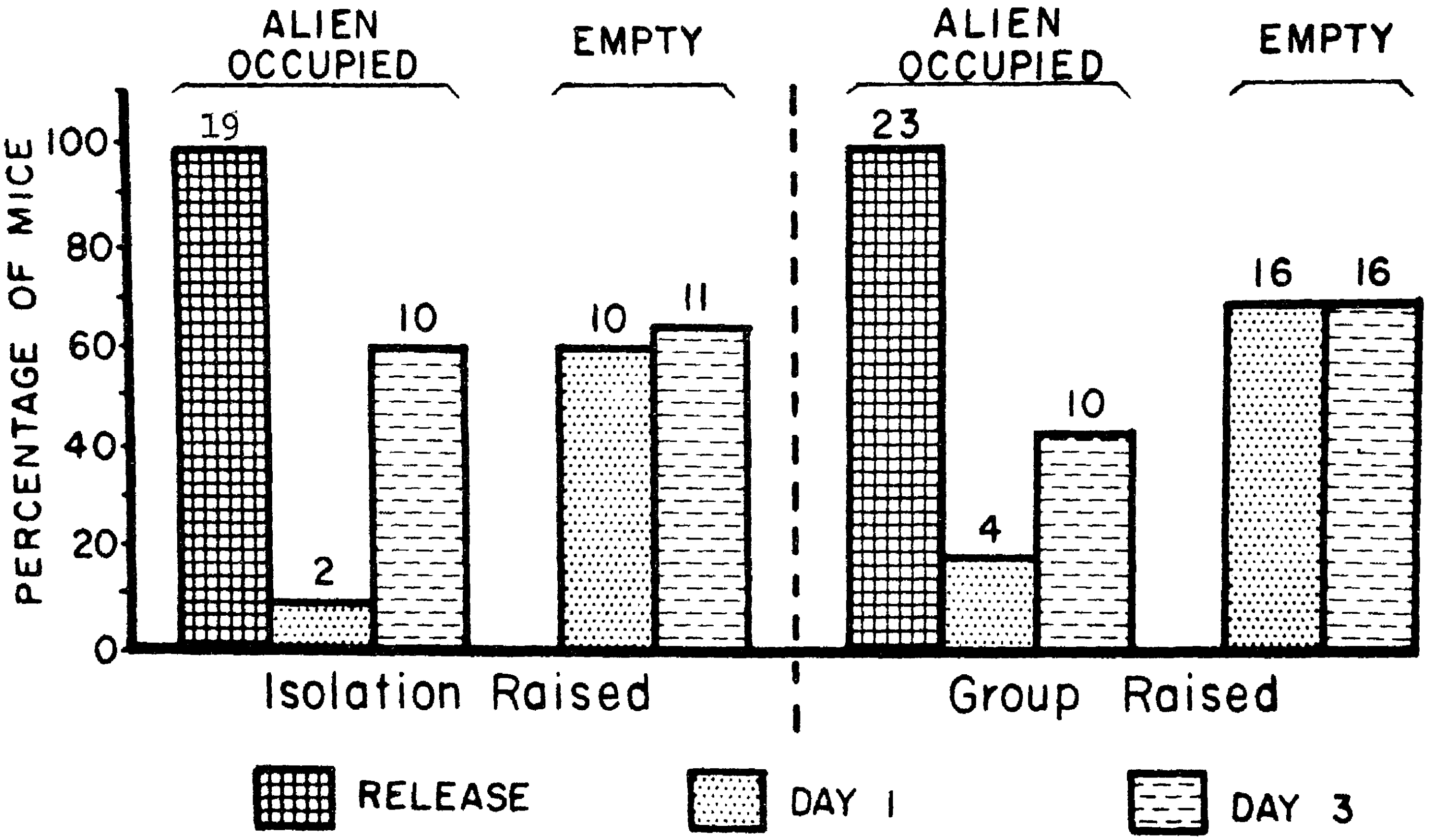

Fig. 22. Percentage of mice found in alien occupied or in empty nest boxes - social treatments.

Table XIX shows the results of statistical comparisons of these data.

TABLE XIX

OCCURRENCE IN EMPTY OR IN ALIEN OCCUPIED NEST BOXES

Comparison	Larger Frequency and Significance	
	Day 1	Day 3
Number occurring in each type of nest box		
Compared with chance ($P=.5$)		
Combined data	$E > O$ $(P < .001)$	
Isolation raised	$E > O$ $(.05 > P > .02)$	
Group raised	$E > O$ $(.02 > P > .01)$	
Comparing numbers found in each type of nest box.		
Combined data	$M > A$ $(P < .001)$	$M > A$ $(.3 > P > .2)$
Isolation raised	$M > A$ $(.01 > P > .001)$	ND $(P > .5)$
Group raised	$M > A$ $(P < .001)$	$M > A$ $(.2 > P > .1)$
Comparing social treatments	ND $(P > .5)$	ND $(P > .5)$

E = Expected frequency of mice in each type of nest box.
O = Observed frequency of mice in each type of nest box.
M = Frequency of mice found in empty nest boxes.
A = Frequency of mice found in alien occupied nest boxes.
ND = Difference in frequencies small or none.

When the social treatments are evaluated separately, the proportion of mice occurring in empty boxes was significantly larger than the proportion in occupied nest boxes for day 1 in both isolation and group raised mice. There was no difference in nest box occurrence by day 3.

These data, therefore, indicate that mice occurred in empty nest boxes significantly more often than expected by chance. On day 1, a significantly greater proportion of mice occurred in empty nest boxes than in boxes occupied for one night by a young, male, alien mouse. By day 3, two days after removal of the aliens, this preference for empty nest boxes had disappeared.

DISCUSSION

Factors affecting populations in the wild are difficult to ascertain experimentally due to lack of control of the experimental situation. Loss of animals due to dispersal (Blair, 1940; Howard, 1949; King and Eleftheriou, 1957) and death from many causes make it difficult to control numbers while studying related variables.

This study was an attempt to combine the laboratory and field approach with a minimum loss of their individual advantages (Schneirla, 1950; Scott, 1950). Thus, the biology of populations, both physical and social, may be studied under semi-natural conditions while maintaining, partially at least, a measure of the controlled conditions enjoyed in the laboratory. Accordingly, the "mouse-proof" experimental field has proven an effective method for studying populations. It appears that this technique has almost unlimited applicability to the study of the population dynamics of small mammals.

The results of these experiments naturally separate into two major frames of reference and will be discussed accordingly. The first area for consideration concerns those data suggesting the existence of phenomena which may be specific to populations of prairie deermice, to mice of the species Peromyscus maniculatus, or that have general significance with regard to small mammals. The second category concerns the differential behavior of the populations as a result of the two social treatments, in which mice were raised in isolation or in groups.

Population Phenomena

Care should be taken in the extrapolation to natural populations of conclusions based upon data obtained under artificial situations. The results discussed here, and the hypotheses suggested by them, may be functions of the experimental situation only.

Movement data. The frequency of moves, and the distance moved to nest boxes during the last 10 days of the period of population establishment, showed that between 55 and 60 per cent of the mice moved to different nest boxes each night. Although more than half of the mice moved to different nest boxes each night, less than half of these moves were to boxes previously unvisited by each mouse. Therefore, while mice moved at a relatively constant rate, they moved less frequently to unvisited boxes, even though there were many available. Thus, each mouse localized to the use of a few nest boxes among which it continued to move.

The commonly accepted concept that an animal maintains one nest site around which its activity centers was contradicted by the evidence cited above. The idea of a single nest site has conceptual value in the explanation of territorial behavior in mammals (Burt, 1940, 1948, p. 21). It may, however, lead to error when dealing with species in which such defense behavior is questionable (Blair, 1940, 1951, 1953b).

The fact that each mouse used an average of 4.3 nest boxes during the last 10 days and subsequently homed to one of these boxes raises two questions. Were these multiple residence sites only a function of the large number of boxes available or was each a home site or a refuge? These questions cannot be conclusively answered here. Howard (1949) studying natural populations of prairie deermice, found that mice living in areas with a large number of nest boxes changed their home sites more frequently than those living where the nest boxes were more widely distributed. Since he visited his nest boxes only once a week, his experiments were not designed so that the number of nest boxes used per mouse could be ascertained. Nicholson (1941) studying the White-footed Mouse (*Peromyscus leucopus noveboracensis*) in the wild, found that mice left the nest boxes after a "short period of residence". During his study, 174 mice were captured more than once in nest boxes. Of these, only 16 lived in a box for more than four consecutive weeks. His data are of questionable significance in this comparison since he, too, checked his boxes only once a week.

Blair (1940), studying prairie deermice found that individuals fled to a number of different holes after their release from live traps. He concluded that each mouse had six or more refuges within its home range, of which an unknown number were permanent homes. His later study (1951) of the Beach Mouse (*Peromyscus polionotus leucocephalus*), indicated that the home range of each mouse contained an average of about 20 holes, of which a mean of 5 were entered by each after release from the traps. The fact that mice stored food and nested there for short periods indicated that these holes were more than refuge holes.

In this study, the mice moved among approximately 5 nest boxes during the last 10 days of each experiment. In those experiments in which some mice disappeared early in the experimental period, no increase was noted in the average number of nest boxes occupied by the remaining individuals. This may indicate that each mouse selected a relatively constant number of boxes to be used as refuges and/or nest sites. Since nest boxes were checked only during the day, there was no way of distinguishing between nest sites and refuges. General nocturnal observations, however, indicated that nest boxes were used for both nest sites and refuges, depending upon the circumstances. As suggested by Burt (1940), it would be of distinct survival value for a mouse to have several nests distributed over the area. It could retreat to them and lessen the chance of death from exposure and predators.

An important difference between the conditions maintained in this study and wild conditions is that the experimental mice did not have young while in the field, although most of the females were pregnant at the end of each experimental period. Certainly, care of a litter and perhaps pregnancy, may cause sedentary behavior resulting in the occupancy of fewer nest boxes.

The possibility should not be overlooked that the daily nest box check caused the mice to move to other nest boxes as frequently as they did. Checking of the nest boxes seemed of little significance, since only half of the mice moved each day. This indicated that movement was a matter of individual behavior. The nest box checks could not have caused the movement unless each examination affected each mouse differently each day.

If mice move between temporary residence sites, home ranges and artificial distribution measurements (Burt, 1940, 1943; Blair, 1940, 1941; Hayne, 1949; Holenreid, 1940; Mohr, 1947; Stickle, 1946) calculated on the basis of a few nights sampling may be greatly in error.

Gregarious behavior. The experimental mice were found alone significantly more often than in combinations. Mice were found in bisexual pairs significantly more often than in any other type of combination. Mice were in bisexual pairs significantly more often than expected by chance or than found in monosexual pairs. Thus, a preference was shown for occurrence alone in nest boxes and for combinations only as bisexual pairs.

The above data illustrate the expected attraction between animals of the opposite sex. The fact that mice of both social treatments occurred alone so frequently, however, was unexpected. Howard's (1949) nest box study suggested that deermice were infrequently found alone in nest boxes, but were usually found in bisexual pairs. Howard (ibid) further noted that when the sex ratio was unequal, several mice of the more numerous sex were simultaneously found with the opposite sex. He does not, however, give frequencies or the exact time of year for these data.

Nicholson's (1941) nest box study indicated that white-footed mice were usually found living singly. Associations with other mice were of short duration and combinations were usually as bisexual pairs. Nicholson's study further revealed that very few associations composed of the same sex were formed during the breeding season. Of those formed, all occurred at the extreme limits of the breeding season. The data reported here were similar to Nicholson's findings. Out of 23 combinations of the same sex, 14 occurred during the last experiment (October 31 - November 21).

These data indicate that during the breeding season, prairie deermice generally are found alone, combine rarely in other than bisexual pairs, and very rarely occur in a nest box with an animal of the same sex. These data may differ from Howard's because of the semi-natural conditions under which these experiments were carried out. Most groups found by Howard were composed of both parents with their offspring. This was impossible under the experimental procedure utilized here and may have resulted in the differences.

Attraction and repulsion between mice. Little information is available regarding the responsibility for establishing or terminating bisexual pair combinations among deermice. Trapping records have been used as evidence that males have a larger home range than females (Burt, 1940; Blair, 1940; 1942). *Peromyscus* males are thought to move more and to greater distances than females (Burt, 1940;

Nicholson, 1941; Blair, 1942). Thus, males would pass through more home ranges of females than females would of males. It might be supposed that males would combine in home sites with females more frequently than the reverse. In this study, however, no significant difference was found as to which sex originated the bisexual pair or which left it first.

When the data measuring succession of mice in nest boxes were examined, it was determined that females succeeded males significantly more often than expected by chance. Males succeeded females less than expected. It is doubtful that these data indicate an avoidance between opposite sexes since the number of bisexual combinations was larger than that of the other combinations. Also, general avoidance of the opposite sex would not have survival value to the species.

The special significance of the behavior noted above is that females succeeded males significantly more than expected. These data indicate that females follow males into nest boxes on successive days more often than males do females. There was no evidence, however, that the females initiated the formation of bisexual pairs. Evidence on this point is obliterated due to the fact that of the 116 records of the first day pairs were found together, 55 occurrences were in nest boxes in which neither mouse was recorded on the preceding day.

As indicated earlier, the frequency of the occurrence of two animals of the same sex in a nest box was significantly less than expected by chance. Monosexual pairs were recorded with significantly less frequency than bisexual pairs. In addition, there were significantly fewer records of animals of the same sex succeeding each other in nest boxes than were recorded for the opposite sex animals. These data suggest that some type of negative force was operating to segregate mice of the same sex spatially. That this separation of like sexes is not merely a result of the lack of sexual attraction between such animals, but operates through some spatially or socially directed behavior pattern, is evidenced by the low frequency with which animals moved into nest boxes occupied on the previous day by like sex animals. These frequencies were significantly less than expected by chance.

No conclusive information is available concerning the territorial behavior of prairie deermice, either in the defined sense of "defense of an area" (Noble, 1939; Greenberg, 1947) or in the less rigid and more dynamic sense discussed by Emlen (1957) and described by Davis (1958), Marler (1956), and Jenkins (1944). No studies of natural populations of the species *P. maniculatus* have reported active defense of a home area by the mice (Blair, 1940, 1941, 1942, 1943, 1951, 1953b; Dice, 1932; Howard, 1949). Territorial behavior has, however, been inferred from live trapping studies of *Peromyscus leucopus* (Burt, 1940, 1949).

Some evidence of a "dynamic" non-aggressive type of behavior leading to apportioning of the area among animals of the same population was collected through direct observations and by the homing test.

Observations made during the preliminary experiments as well as during the experimental periods discussed here, indicate that when animals met in the field, both jumped and ran away from each other. Occasionally one mouse chased another mouse a short distance. Observations of social interaction between residents and aliens while aliens were tethered at the feeding stations or at the home nest sites of residents, indicated that residents predominately avoided or ignored the aliens. In the few cases (5) when the residents attacked the aliens, the attacks were of short duration and were terminated by the residents leaving the area. Laboratory studies (King, 1957) of _P_. _m_. _bairdii_ showed single males to be relatively non-aggressive toward other males. Terman (1958) found single females to be slightly more aggressive than single males when aliens were placed in their home mouse boxes. The incidence of attacks was very low for both sexes, however. When these same males and females were paired and then aliens placed in the mouse box, the number of attacks by residents greatly increased and the males were usually the attackers. Such aggression by the male was usually of short duration. In these laboratory experiments, neither the resident or the alien could leave the mouse box, so fighting was generally terminated by the alien assuming a defense position and the resident hesitating to attack. In the experiments in the field, however, the residents were free to leave the area and did so.

The results of the homing experiments with aliens in the field further elucidate this problem. Homing to alien-occupied nest boxes while young aliens were in the field, was significantly less than that observed before aliens were in the field. This was true for both social treatments. Avoidance of aliens was further demonstrated by the occurrence of the mice in empty nest boxes significantly more often than in alien occupied boxes. These data indicate that spatial distribution may be affected through avoidance or some unmeasured negative force between animals (Howard, 1949). Prior occurrence (Braddock, 1949) or merely presence in the area may be the important factors.

With regard to the question of territoriality, then, no reliable evidence for active defense of an area was shown. Animals of the same sex may be spatially segregated as a result of a negative repulsive force, hypothetically, avoidance.

Homing. Homing ability in species of Peromyscus has been demonstrated in many studies (Burt, 1940; Johnson, 1926; Kendiegh, 1944; Murie and Murie, 1931, 1932; Stickle, 1949}. Murie and Murie, (1931) reported a few mice returning from distances of two miles and many returning from shorter distances. Homing success in the above mentioned studies was measured by capture of mice in traps in their inferred home areas subsequent to their release at varying distances. As such, the above studies have measured the return of Peromyscus to a home area.

Homing was used in this study to measure the significance to the mice of the previously established spatial distribution patterns, as shown by their ability to home to a few specific nest boxes. Also, the homing performance before aliens were in the field was compared with the homing performance after aliens were temporarily in the field.

Both socially treated populations homed significantly more often than expected by chance. This indicated that the mice were able to traverse at least half the length of the experimental plot, bypass numerous nest boxes, and return to one of the few (4 or 5) boxes previously occupied. Further, mice that did not home by day 1 frequently did so by day 3. Such performance indicated that the individual mice recognized both their "own" nest boxes and the nest boxes of their neighbors.

These homing data may be indicative of the existence of some sort of spatial framework or "positional stability" (Orr, 1955) as a characteristic of each population. Howard (1949) and Dice and Howard (1951) found little tendency for prairie deermice to move from home areas once they had bred there. Studies of natural populations of Peromyscus have shown that removal of all individuals living within a specified area was followed by immigration to the vacated area by mice living in adjacent areas (Blair, 1940; Calhoun and Webb, 1953; Stickle, 1946). Such behavior is an indication of the part social interaction may play in the distribution of mice. Orr (1955) suggested that animals were aware of neighboring individuals living around the periphery of their home range and when these neighboring animals were removed by one cause or another, the social stimuli were also removed, with the result that the remaining animals expanded their ranges.

Introduction of 3 week old, alien males into the home nest boxes of residents disrupted homing per se for both social treatments. There was no significant difference between the homing performance of mice from either social treatment following the introduction of aliens. Examination of the homing data following introduction of aliens revealed that the decrease in homing success was due to differential homing to nest boxes occupied by aliens and to boxes in which aliens had never been. The data indicate that the difference in homing performance after aliens were introduced was primarily due to the poor homing success of mice returning to alien occupied nest boxes. The importance of social behavior as a determiner of spatial distribution is, therefore, evident. The influence of social factors was further demonstrated by the few occurrences of residents on day 1 in any nest boxes occupied by young aliens.

What significance does the avoidance of aliens have in relation to the spatial distribution within local populations and to the geographical distribution of prairie deermice? The data collected in this study suggest that spatial distribution may be achieved by mutual avoidance between animals of like sex. Statements regarding heterosexual interaction should not be made on the basis of the evidence available. Further, such interactions affecting spatial distribution undoubtedly vary. Estrus and the care of young, no doubt, affect female distribution patterns. A population of prairie deermice may space itself as a result of some intrinsic mutual repulsion mechanism which is adjusted to the physical as well as the biotic environment, and is not a function of territoriality in the defined sense. Such a mechanism was discussed by Frank (1957) for Microtus arvalis and Microtus agrestis and termed the "condensation potential". The importance of individual behavioral differences within this concept was discussed in the introduction of this paper.

Spatial distribution through mutual avoidance of individuals would appear to be of at least equal adaptive significance to the biology of the population as that suggested for territoriality by Burt (1949). Mutual avoidance behavior would achieve distribution in accordance with the carrying capacity of the environment without the wounding and deleterious effects of fighting (Clarke, 1955; Calhoun, 1950, 1952) and social stresses (Christian, 1956, 1957). Such lack of overt aggressinn among prairie deermice has been previously pointed out in this study and in a laboratory study by King (1957). King mentioned that in confined P. m. bairdii males used in his tests "frequent nosing and grooming behavior suggested dominance without a fight".

Howard (1949) studying dispersal from birth place to breeding site showed that 119 or 76% of 150 young deermice moved less than 500 feet from the site where they were born before breeding and nesting. These data were biased by the fact that the greater the distance the mice moved, the less chance there was of their being recorded in nest boxes again. The proportion of mice moving this short distance from birth site to breeding site, however, is indicative of a short dispersal pattern (Dice and Howard, 1951; Blair, 1953b).

It is of further interest that evidence exists for a major range extension of P. m. bairdii and of the species P. maniculatus in recent times (Blair, 1953a, 1953b). Extension of the range of the local population of prairie deermice as well as the geographical distribution of the species may be largely through a diffusion-like process rather than by long individual moves. Young animals, upon leaving the nest may move into an occupied area or into a temporarily empty nest site rather than making long moves until an unoccupied area is found. Such behavior could cause a partial displacement of the residents due to avoidance behavior, and result in a gradual extension of the range at the periphery.

Social Behavior

In the previous section, it has been shown that social interaction between animals is important in determining spatial distribution within local populations. This study was designed to manipulate two social variables and measure their differential affects upon the spatial distributions of mouse populations under semi-natural conditions. While some measurements revealed behavioral patterns which were unaffected by the social manipulations and apparently were characteristic phenonomena of the populations, other measurements showed a consistent difference between the populations raised in groups and in isolation.

The measurements of gregarious behavior indicated that isolation raised mice were recorded alone in nest boxes proportionately more often than group raised mice. The reciprocal of this significant result is that the proportion of nest box records in which one mouse was combined with at least one other mouse was higher for group raised mice than for isolation raised mice.

No significant differences were found between social treatments when comparing various data having to do with bisexual combinations, although consistent trends were noted. Group raised mice were consistently different from isolation raised mice in that a higher proportion combined with the opposite sex, they were found in a larger number of different combinations, and they continued in combinations for a longer period of time.

Group raised mice combined with the opposite sex significantly sooner after introduction into the plots than did isolation raised mice.

Daily comparisons of the average distance between the nearest neighbors of the same, opposite, or either sex showed that isolation raised females were consistently and significantly further away from their neighbors than group raised females. Isolate male mice were significantly further from females than group raised males. Group raised males were further from other males than isolate males were, but not significantly so $(.1 > P > .05)$. It is possible that there was a differential sex affect of the social treatment which an eventual analysis of the data will reveal.

The homing performance after aliens were introduced to the nest boxes showed no difference between social treatments in homing per se, to nest boxes in which aliens had never been placed, or to alien occupied nest boxes. Mice of both social treatments homed to alien occupied nest boxes significantly less frequently than they did when homing was established as a phenomenon. Group raised mice showed no significant difference between their established rate of homing and their homing performance to alien-free nest boxes after the aliens were in the field. During and following the time aliens were in the field, however, isolation raised mice homed significantly less often to boxes which never received aliens than was the case in the homing establishment experiments. The significant difference between pre and post-alien homing performance to empty nest boxes for isolation raised mice, was due to their better homing performance as compared to that of the group raised mice during the experiments before aliens were in the field.

Thus, the introduction of aliens to half the nest boxes had a more adverse affect upon isolation raised mice than group raised whether they were homing to empty or alien occupied nest boxes.

Group raised mice homed to empty nest boxes significantly more than to alien occupied on day 1 only. Isolation raised mice did not home with a significantly different frequency to either type of nest box. There were no significant differences between social treatments in the number of mice found in empty or alien occupied nest boxes.

The comparison of social treatments during the experiments when homing was established as a phenomenon showed that although mice of both social treatments homed by day 1 significantly more often than expected by chance, the isolates homed significantly better than the group raised. Not only did isolates home more often than group raised mice but the difference in homing performance between the two social groups was greater and was significant at a higher level of probability on day 3 ($.01 > P > .001$) than on day 1 ($.05 > P > .02$). Thus, it appears that isolate animals which did not succeed in homing on day 1 sought to return to a previously occupied box by day 3 more often than did the group raised mice.

A summary of the behavioral characteristics of isolation raised mice as opposed to group raised mice is as follows: the isolation raised mice combined with others less often than the group raised; were slower in combining; generally, with few exceptions, maintained a greater distance from their fellows; and homed significantly more often.. Differential homing behavior after aliens were in the field, showed isolation raised mice to be more adversely affected by the introduction of aliens than were group raised mice. Isolation raised mice thus appeared to be less sociable and more spatially oriented than group raised mice.

Few studies of the affect of isolation upon social behavior have been made among mammals (Beach and Jaynes, 1954). King and Gurney (1954) and King (1957) reported that male C57BL/10 mice, raised in isolation from weaning, were less aggressive than their controls raised in social groups. Kahn (1954) found that male *Mus* raised in isolation from weaning were more aggressive than males raised with their mothers. King and Eleftheriou (1957) raised *Peromyscus* in isolation and in groups and then released them into the wild in an effort to ascertain the affects of social experience upon adaptation to the natural environment. They were greatly hampered by a precipitous decline in the populations by the end of the first week, but observed that isolation raised mice were found together in nest boxes less frequently and moved about the field more and to greater distances than group raised.

With the above facts in mind, the greater homing performance of isolation raised mice may be hypothetically explained in the following manner: spatial and social patterns of distribution were of greater significance to the isolation raised mice. As was pointed out earlier, mice and perhaps other small mammals, may maintain a positional stability or equilibrium. Isolation raised mice, after once establishing themselves in a few nest boxes, seek to return to this social and spatial equilibrium to a greater extent than the more sociable group raised mice. This is undoubtedly not an active seeking but rather that the balance of social and spatial stimuli is not similar to earlier adapted levels until the mice are back in their home areas. Since group raised mice are socially better oriented, adjustment to different social and related spatial stimuli may be more easily made.

The fact that there was no difference in homing behavior between isolatinn raised and group raised mice after aliens were in the field, while there was a significant difference before aliens, signifies that the introduction of aliens had a more adverse affect upon the homing of the former. The lack of homing difference between social treatments after aliens indicates that the avoidance of aliens or alien occupied nest boxes may be a natural population phenomenon, and that the basic spatial equilibrium pattern existent in the study area before introduction of the aliens had been disrupted.

As was mentioned earlier, homing with aliens in the field took place in a series of experiments immediately following those establishing homing as a phenomenon. The difference in the time when each series of experiments was performed cannot be considered influential in the poorer homing performance while aliens were in the field, since the group raised mice showed no reliable differences in homing to empty nest boxes before or after aliens.

Social behavior, therefore, may be an influential force shaping spatial distribution patterns within populations. Social forces may operate as general behavioral characteristics, e.g., territorial behavior, the condensation potential of the species, or they may be effective through individual intrinsic behavioral differences (Christian, 1957; King, 1957; Southwick, 1955; Wellington, 1957).

It is not inoonceivable that wild, free-living mammals may experience behavioral manipulation no less rigorous than the techniques employed here. Such behavioral variations would have great importance in the genetics, evolution, and dynamics of populations.

SUMMARY

Successive populations of Prairie Deermice were raised in the laboratory in isolation or in groups. The affect of the social treatments upon the subsequent spatial distribution of the mice in a semi-natural environment was studied. There were eight experimental periods, each of three weeks duration between June 6 and November 21, 1958. During this time, 8 populations of four bisexual pairs, raised either in isolation or in groups, were living in each of the two 0.44 acre plots of the experimental field.

For 17 days following the release of the mice into the plots, their daily occurrence in nest boxes was recorded. At this time all mice were removed from the plots and kept in isolation in the laboratory for 36 hours. Each was then reintroduced into its home plot at a point distant from its previously established home area. The location of each mouse for the nest three days was recorded. In the last 3 experiments, young alien mice were retained in one-half the nest boxes during the first night after reintroduction of the residents.

The "mouse-proof" field proved to be an effective method for the study of population dynamics under semi-natural conditions while maintaining a measure of the controlled conditions which are possible in the laboratory.

The following are phenomena noted in this study which may be specific to populations of prairie deermice, to mice

of the species *Peromyscus maniculatus*; or which may have general significance to small mammal populations:

a. Between 55 and 60 per cent of the mice moved to different nest boxes each night. Less than half of these moves were to boxes previously unvisited by the mouse moving. Therefore, each mouse localized and used a few nest boxes among which it continued to move. These data indicate that each mouse maintained several refuges and/or nest sites rather than a single one around which its activity centered. Such behavior should be considered when measurements are made of the spatial patterns of individual animals in the wild.

b. During the breeding season, the prairie deermice in this study were generally found alone or in bisexual pairs, combined rarely in other than bisexual pairs, and very rarely occurred in a nest box with an animal of the same sex.

c. No conclusive evidence was obtained as to which sex originated or terminated bisexual pairs.

d. Mice of the opposite sex succeeded each other in nest boxes significantly more often than those of the same sex. Females followed males into nest boxes on successive days significantly more often and males followed females significantly less often than expected by chance.

e. No reliable evidence for territoriality as defense of an area was obtained. The data suggest that animals of the same sex may be spatially segregated as a result of a negative repulsive force, hypothetically, avoidance.

f. Mice of both social treatments homed to previously occupied nest boxes significantly more often than expected by chance. This indicated that the individual mice recognized both their "own" nest boxes and those of their neighbors. Thus, some sort of spatial distribution framework or a "positional stability" may be a characteristic of each population.

g. Mice of both social treatments homed significantly less often to nest boxes temporarily occupied by young aliens than they did in the experiments prior to the introduction of aliens. This significant decrease in homing supports the hypothesis that the spatial distribution of prairie deermice may be achieved through a mutual avoidance of individuals. Extension of the range of the local population as well as of the geographical distribution of the species may be largely through a diffusion-like process rather than by long individual moves. Young animals, upon leaving the nest may move into an occupied area or into a temporarily empty nest site rather than making long moves until an unoccupied area is found. Such behavior could cause a partial displacement of the residents due to avoidance and would result in a gradual extension of the range at the periphery.

The differential effects of the social treatments were as follows:

a. The isolation raised mice combined with others less often than the group raised mice; were slower in combining, and generally, maintained a greater distance from their fellows.

b. Isolation raised mice homed significantly more often than group raised during the experiments when homing was established as a phenomenon. The introduction of aliens into one-half the nest boxes had a more adverse affect upon the homing performance of isolation raised mice than upon that of group raised.

c. Isolation raised mice appeared to be less sociable and more spatially oriented than group raised mice.

d. The data suggest that spatial patterns of distribution existent in the plots were largely determined by social interaction and were of greater significance to isolation raised mice than to group raised. Isolation raised mice adapted less easily to changes in the social and related spatial stimuli than the more sociable group raised mice and, thus, more frequently returned to the earlier established patterns of spatial and social stimuli. The introduction of aliens disrupted the social-spatial equilibrium existent in the plots. This disruption had a more severe and longer lasting affect upon isolation raised mice than upon group raised due to the inability of the former to quickly adapt to the environmental changes.

d. Differences in social behavior have been shown to be important factors determining spatial patterns of distribution within local populations. The importance of social factors to the evolution, genetics, and dynamics of populations was also suggested.

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