This is to certify that the

thesis entitled

DISPERSAL OF PEROMYSCUS LEUCOPUS
WITHIN AND BETWEEN WOODLOTS

presented by

Richard Robert Tardif

has been accepted towards fulfillment
of the requirements for

Ph.D. degree in Zoology

John A. King
Major professor

Date 30 July 1979

DISPERSAL OF *PEROMYSCUS LEUCOPUS* WITHIN AND BETWEEN WOODLOTS

By

Richard Robert Tardif

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Zoology

1979

ABSTRACT

DISPERSAL OF *PEROMYSCUS LEUCOPUS* WITHIN AND BETWEEN WOODLOTS

By

Richard Robert Tardif

The general hypothesis tested was that white-footed mice (*Peromyscus leucopus*) which disperse across a barrier (habitat not usually occupied by the species) differ qualitatively from conspecifics which disperse within continuous habitat. Dispersal was defined as immigration onto an area from which all *P. leucopus* had been removed. There were three experimental groups. Isolated immigrants were trapped in small woodlots which were surrounded by fields. Contiguous immigrants were trapped in areas equal in size to the woodlots from which isolated immigrants were taken; these were located in the center of larger woodlots. Mice could invade these areas while remaining in forested habitat. Residents were the mice removed from the above areas in the first week of trapping.

Demographic characteristics of the three groups were investigated by removal trapping for 28 consecutive days in June and September for two years. Age, as measured by eye lens weight, was the only variable that consistently distinguished the two immigrant groups. Isolated immigrants, contiguous immigrants, and residents did not differ in the proportions of adults and juveniles (age classes determined by body size). However, among adults, isolated immigrants had significantly

lower eye lens weights than contiguous immigrants and residents, which were equal. The proportions of males and females did not differ among the groups in any trapping period. Residents showed high reproductive activity in all four trapping periods. Isolated immigrants were as reproductively active as residents in June, and significantly less so in September. Contiguous immigrants were also inactive in September, but were reproductively active in one June and inactive in the other. The majority of adult female isolated immigrants in June were pregnant.

Behavioral tests were conducted in the laboratory on wild-caught members of the three experimental groups trapped at other times. When given the opportunity to traverse barriers in the laboratory, isolated immigrants crossed in significantly greater numbers than contiguous immigrants and residents, which did not differ. When exposed to a choice of water and a novel solution, isolated immigrants showed significantly less neophobia than contiguous immigrants and residents, which did not differ. When consumption of four foods was monitored for six days, the feeding diversity of the two immigrants groups did not differ, but immigrants were significantly more diverse than residents.

The development of barrier crossing, neophobia, and feeding diversity was studied in F_1, laboratory-reared P. leucopus. Mice about 44 days of age did not differ from mice at about 90 days when tested in the barrier apparatus. Similarly, age did not affect neophobia. However, mice exposed to five different novel flavors from 21-40 days of age were significantly less neophobic at 44 days than mice which received only water. This difference disappeared if testing was delayed for six weeks after the experience was administered. Early experience also affected feeding diversity. Mice reared with an unpredictable diet were significantly more diverse at testing than mice raised on stable diets. Weanlings and adult mice raised on laboratory chow did not differ. For all three behaviors, males and females behaved alike.

P. leucopus which have dispersed between woodlots possess a constellation of characters that distinguishes them from mice that have dispersed within continuous habitat. Although isolated immigrants are younger, age itself is not sufficient to account for the observed behavioral differences. Rather, _P. leucopus_ change their behavior in response to experience; such behavioral plasticity would probably benefit an individual attempting to become established in a new area. The dispersal of highly reproductive, behaviorally plastic individuals to isolated patches of habitat in spring could result in rapid exploitation of habitat.

To

Ma and Vic

ACKNOWLEDGEMENTS

I thank John A. King for his guidance and patience throughout my training, and James L. Edwards for his counsel and friendship both on and off campus. Rollin H. Baker and Stephen N. Stephenson provided valuable advice as members of my guidance committee.

I thank the graduate students of the Animal Behavior Group and The Museum for our discussions. Carolyn Bunting, Anne Cloutier, Deborah Dietrich, Mark Hatch, Michele Mitchell, and Carolyn Wooley all assisted in the collection of data; and to them I am grateful. My special thanks go to Gale Haigh for his dedication throughout the field work.

Suzette Davis supplied moral support and technical assistance that made the completion of this study possible.

My financial support and funding for the animal colony were provided by the Department of Zoology and NIMH grant #MN-29414. Computer facilities were provided by the University.

TABLE OF CONTENTS

Page

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Dispersal is the movement in which an animal leaves its home area and attempts to establish a new one (Lidicker, 1975). Such movements are a factor in gene flow between local populations and in the regulation of the size of populations. Through dispersal, suitable but vacant areas become populated, and the range of the species is extended. An individual, by dispersing, may escape unfavorable aspects of its environment and increase its chances of reproducing, but the associated risks are high. For a more thorough discussion of the consequences of dispersal, see the Literature Review (below).

The dispersal of individual organisms is inhibited by barriers, that is, areas of inhospitable habitat. Even in relatively homogeneous habitat, barriers may be imposed by unfamiliar areas, hostile social interactions, competitors, and predators. Dispersants are distinguished on the basis of their attempts to move through these areas. It is important to realize that all normal, healthy members of a population (except nestlings) are physically able to cross such barriers. Barriers act by limiting the type of individual that will cross them.

Dispersants may cross different types of barriers. Most environments are, to some extent, heterogeneous, providing dispersants with a choice of crossing or not crossing types of habitat in which they would not otherwise reside. These habitats are the physical and ecological features most commonly recognized as barriers. The greater the extent and divergence of these areas from that of the home range, the more severe is the barrier. A field may be a barrier to a woodland form, a forest may be a barrier to a grassland form, and a stream or pond may be a barrier to a terrestrial form.

Among dispersants, then, some will move within continuous (relatively homogeneous) habitat and others will traverse types of habitat in which they would not otherwise occur. These habitat discontinuities function by imposing selection for the types of individuals that are willing to cross. The basic hypothesis of this dissertation is that individuals that disperse across habitat not usually occupied by the species will differ qualitatively from conspecifics which disperse within continuous habitat.

In south-central Michigan, forested areas often occur as woodlots surrounded by fields. Woodland forms dispersing under these conditions have the options to disperse within the woodlot in which they occur or to disperse between woodlots. *Peromyscus leucopus noveboracensis* (Mammalia: Cricetidae) is a common occupant of these woodlots. It occurs predominantly in forested or brushy areas (Beckwith, 1954; Burt, 1957; Burt and Grossenheider, 1976; Hall and Kelson, 1959). *P. leucopus* was chosen as the species for this study because (1) fields between woodlots represent habitat discontinuities which the mice could choose to cross or not cross, (2) the species occurs in sufficient numbers, (3) it is easily trapped, and (4) a reasonably large body of data exists on the natural history of the species.

The distance between available woodlots varied. In this study, a barrier was operationally defined as 100 m of agricultural field or pasture devoid of trees and shrubs. This distance was chosen because (1) it was attainable in the study area available, and (2) it is larger than the distance usually covered by these mice within their home range in a forest but (3) within the dispersal range of the species, so that a sufficient sample could be obtained (see Dice and Howard, 1951; Nicholson, 1941; Stickel, 1968). Dispersal (immigration) was operationally defined as capture on an area from which all _P. leucopus_ had previously been removed.

Chapter 2 of this dissertation deals with the demographic characteristics of the two immigrant groups and residents. The variables examined were age, sex, and reproductive condition. Specific hypotheses regarding each of these variables will be presented here.

Both adult and juvenile _P. leucopus_ are known to disperse (Fairbairn, 1978a; Harland _et al._, 1978; Stickel, 1968; Terman, 1968). Young mice leave the parental home range just prior to the age of sexual maturation and establish a home range of their own (Burt, 1940; Nicholson, 1941; see also Literature Review, below). It has also been demonstrated that, in continuous habitat, creation of a depopulated area causes some individuals outside of the removal area to move into the vacant area (Calhoun, 1963; Calhoun and Webb, 1953). The invading animals included adults that previously had established home ranges (Stickel, 1946; Van Vleck, 1968). Apparently, some otherwise sedentary members of a species, including _P. leucopus_ will disperse to fill vacant areas in continuous habitat.

According to the information above, _P. leucopus_ that invade a vacant area in continuous habitat should include both juveniles and adults. Adults would be expected to make movements in response to local vacancies; juveniles leaving the parental home range would also be expected to invade such areas. Adults would not be expected to move in response to vacancies in another woodlot because they are unaware of them but juveniles -- animals that would be dispersing anyway -- would move to such areas. From this the hypothesis follows that *P. leucopus* which disperse across barriers will be younger than those dispersing within continuous habitat.

Male *Peromyscus* tend to disperse farther than females (e.g. Dice and Howard, 1951); thus a small surplus of males might be expected in immigrants which cross barriers. Males tend to have larger home ranges than females (see Stickel, 1968); therefore it is likely that more males than females will find and invade a vacant area. In addition, most populations of *Peromyscus* have a surplus of males (i.e. sex ratio > 1) (see Terman, 1968). In terms of sex distribution, then, both immigrant groups should have more males than females. Males generally outnumber females among dispersing *Peromyscus* (Dice and Howard, 1951; Fairbairn, 1978a; Harland *et al.*, 1978; Stickel, 1968; Vessey and Mitchell, 1978). There is, however, no basis to hypothesize a difference in sex ratio between the two immigrant groups.

If most dispersal occurs prior to or at the age of puberty, then immigrants should show little reproductive activity. Indeed, all of the *Peromyscus maniculatus bairdi* studied by Howard (1949), except one male, dispersed prior to achieving sexual maturity. If, on the other hand, adults move into vacant areas, we would expect their reproductive condition to correspond to that of the residents. Fairbairn (1977) found some immigrants to be sexually mature, although most males were not (see also Harland et al., 1978). Thus according to the predictions regarding the ages of immigrants, mice crossing barriers should be less reproductively active than mice dispersing within continuous habitat.

In summary of the demographic variables, the hypotheses were these: Peromyscus leucopus which disperse across a barrier to ecologically isolated habitat will be younger and less reproductively active than conspecifics invading vacant areas without leaving habitat normally occupied by the species. The groups will not differ in the distributions of the sexes.

Chapter 3 of this dissertation concerns laboratory investigations of behavioral differences between the two immigrant groups. The behaviors examined were barrier-crossing, neophobia, and feeding diversity. The hypotheses regarding each of these are discussed here; for a general discussion of the behavioral characteristics of dispersants, see the Literature Review (below).

The two immigrant groups are, by definition, distinguishable according to movement across a barrier in the field. Given an opportunity to cross a barrier under controlled conditions in the laboratory, immigrants that have moved between woodlots might be expected to cross significantly more often than either residents or within-woodlot dispersants. In essence we are asking whether or not the distinguishing characteristic from the field can be replicated under other conditions. If it can, the basis for distinguishing these two groups as different would be reinforced.

Neophobia is the tendency of animals to avoid novel edibles or objects, and its occurrence is well documented in the literature (see Domjan, 1977). If an animal does not eat a novel food it is safe from negative effects such as poisoning, but its risks hunger and the loss of available food. The consequences of eating novel food range from satiation of hunger and discovery of a new food to death. Therefore, an animal's response to a novel food is important.

In all probability, immigrants encounter novel foods. Their willingness to eat them may directly affect their chances of survival. Moreover, mice dispersing within a woodlot are less likely to encounter novel foods than mice dispersing to a different woodlot. The hypothesis was tested that P. leucopus which disperse across a habitat discontinuity are less neophobic than conspecifics which have dispersed within continuous habitat.

Animals differ along a continuum in the diversity of their diets from generalists to specialists (Klopfer, 1973; MacArthur, 1972; Morse, 1971; Rozin, 1974). Generalists are those animals that eat a wide variety of foods and thus have broad feeding preferences. Specialists, in contrast, eat only a few types of food and thus have narrow preferences. The final hypothesis regarding behavioral differences between the two groups is that feeding diversity will differ.

An immigrant encounters a food supply that is unknown in location and quantity; and if the new habitat differs from that previously inhabited, the quality of potential food is also unknown. That is, the environment is relatively unpredictable to an immigrant. Conversely, an established resident is probably more aware of what foods are available to it. Between these extremes we might expect that an individual which disperses within continuous habitat would encounter habitat more similar to that of its previous home range than an animal which disperses between patches of habitat. Familiarity with the food supply will be increased by the similarity of the new and old home ranges. That is, for these groups, the predictability of the food supply will be positively correlated with the familiarity with the new home range.

Most models of resource exploitation strategies state that generalist feeders will occur in unpredictable environments (Klopfer and MacArthur, 1960; MacArthur and Levins, 1967; Oster and Heinrich, 1976; Randolph, 1973). Thus the hypothesis was tested that mice which invade an area by crossing a physical barrier will have more diverse feeding preferences than animals invading an area within continuous habitat, and both of these groups will exhibit more feeding diversity than residents.

In summary of the behavioral variables, then, the hypotheses tested were these: in the laboratory, immigrants which have crossed a barrier in the field will be less neophobic, exhibit higher feeding diversity, and will cross a barrier in greater numbers than immigrants which have dispersed within continuous habitat.

Chapter 4 of this dissertation deals with the origin of the behavioral differences observed in Chapter 3. Behaviors are phenotypic expressions of both genetic and environmental influences (Lehrman, 1970). Investigation of the role of genetics would require long-term experiments on selection and heritability (Alcock, 1975; Brown, 1975). Instead, I chose to examine the role of factors that occur within the course of an animal's lifetime. The specific factors examined depend to some extent on the results of the demographic and behavioral results presented in Chapters 2 and 3; therefore a discussion of the specific hypotheses concerning the role of these factors in the barrier-crossing, neophobia, and feeding diversity will be deferred to the introductions to the specific experiments.

CHAPTER 1

LITERATURE REVIEW

DISPERSAL IN SMALL MAMMALS

Definitions and Measurement

Dispersal can be defined as the movement from the natal site to the place where an animal reproduces (Howard, 1949). This definition was commonly used in the early years of the study of small mammal population dynamics. It is consistent with the view that mice leave the parental home range, establish a home range of their own, and remain relatively sedentary thereafter (Burt, 1940; Howard, 1949, 1960; Metzgar, 1971; Nicholson, 1941). However, a more dynamic view of dispersal is currently held because animals often change their home range at other times for a variety of reasons (Bekoff, 1977; Smith, 1978; see also Initiation of Dispersal, below). Recognition of these movements has resulted in broadened definitions of dispersal. Brown (1975, p. 49) defined dispersal simply as "movements of animals from a source..." Lidicker (1975, p. 104) defined dispersal more specifically as "any movements of individual organisms... in which they leave their home area, sometimes establishing a new home area... (excluding) short-term exploratory movements." I will consider dispersal according to Lidicker's definition, which provides latitude in the causation and timing of the phenomena to be considered, but specifies at least an attempt by the animal to permanently move its home range.

Explicit in the concept of dispersal is the idea that an individual initially has a home range, then leaves it, wanders for a time, and ultimately establishes a new home range. Ideally then, when one studies dispersal, these behaviors should be observed if an individual is to be considered a dispersant. In reality this entire sequence is rarely seen for a number of individuals. Of the animals that disappear from a study area, some have died *in situ* and some have emigrated. Of those that emigrated, some die before establishing a new home range and some move off of the study area. Conversely, animals that appear in a monitored area may either be immigrants or animals born on the study area. The entire dispersal sequence is nearly impossible to observe in significant numbers. Researchers usually study segments of the dispersal sequence and infer the remainder.

Garten and Smith (1974) studied dispersal in the old-field mouse (*Peromyscus polionotus*) by installing a drift fence and examining the animals that left and entered the study area. Briese and Smith (1974) similarly studied the movements of several mammalian species. Rowe *et al.* (1963) surrounded corn ricks with metal walls and immigrants and emigrants were caught in live-traps set in holes in the walls. Implicit in this technique is the assumption that mice caught by these methods are actually attempting to enter or leave the study area.

Transients, animals that appear on a study grid for a short time and disappear, provide some data (M'Closkey, 1972; Newsome, 1969). These animals are presumably "passing through" in the process of dispersing, but little is known of their origin, condition, or fate. Fairbairn (1977, 1978a) compared transients on a live-trap grid with immigrants to a removal grid in an attempt to distinguish mortality and emigration.

Among relatively visible animals such as ground squirrels, the disappearance of individuals has been linked to the social milieu of the population (Armitage, 1977; Dunford, 1977; McCarley, 1966; Michener and Michener, 1977; Slade and Balph, 1974). Again, however, the actual fate of most disappearing individuals is unknown (Slade and Balph, 1974; Steiner, 1972).

Howard (1949) overcame many of these problems by providing nest boxes to a free-ranging population of _Peromyscus maniculatus bairdi_; Nicholson (1941) similarly studied _Peromyscus leucopus_. Monitoring the populations in this way provided information on the social history and movements of many individuals. However, many long-distance dispersers are still lost to study. Other species of small mammals (e.g. _Microtus_ spp.) do not use nest boxes supplied in the field.

Dispersal may also be studied by examining the individuals that arrive on a study area. If the resident population is left intact, recruited animals may be immigrants or the offspring of residents, and these two groups are difficult to separate. This method does, however, provide information on the factors influencing recruitment (Boonstra, 1978; Fairbairn, 1978a; Hansen and Batzli, 1978; Harland _et al._, 1978; Sullivan, 1977). The removal of residents and the capture of subsequent immigrants precludes the appearances of animals born on the study area, but the assumption must be made that immigrant are indeed individuals on a one-way movement, not animals making exploratory forays. Monitoring of populations close in time or space to the removal area can provide data on the source of animals captured on the removal grids (Fairbairn, 1978a; Joule and Cameron, 1975; Krebs _et al._, 1976; Myers and Krebs, 1971).

Immigrants may be removed continuously or at regular intervals. Removal at bi-weekly or monthly intervals may allow some establishment of a population of recently-immigrated residents, but immigrants could still arrive just prior to being removed. Also some animals quite probably remain on the study area for several weeks before being removed, and may be in considerably different condition at capture than at the time of arrival. With continuous removal, animals are presumably caught after spending relatively little time on the area. This allows for little change in condition from the onset of dispersal to capture.

Finally, invaders allowed to remain on the study area, and factors influencing the establishment of recruits in the population (Boonstra, 1978; Hansen and Batzli, 1978) can be studied. Andrzejewski and Wroclawek (1962) compared the numbers of animals invading a depopulated area with the numbers settling in a similar area as a function of phase of the population cycle.

As a final factor in studying dispersal, the type of data that can be collected from individuals using various techniques should be considered. The success or failure of immigrants in settling and reproducing can only be obtained from live animals in the field. Behavioral tests and blood samples for genetic or hormonal assays likewise dictate the use of live animals.

Measures of demographic variables that can be made on live animals may lack both precision and accuracy. Body weight and pelage may be used as indices of age, but they only permit the grouping of animals into broad classes, usually with some overlap (Pucek and Lowe, 1975). A similar problem occurs in the measurement of male reproductive condition, where the scrotal or abdominal position of the testes are used to infer reproductivity or non-reproductivity, respectively. Jameson (1950) critically reviewed this practice. For females, pregnancy does not become obvious externally until relatively late in gestation, and the occurrence of previous litters is undetectable. Perforation of the vagina may be used to indicate the achievement of puberty (Rogers and Beauchamp, 1974), but provides no information as to whether or not the animal has actually bred.

Postmortem examinations can provide more detailed data on some demographic characteristics. Age can be measured with relatively high precision and accuracy by the weight of the eye lens, closure of epiphyseal plates, and dental annulations (Pucek and Lowe, 1975). Male reproductive condition can be directly determined by microscopic examination of the testes and epididymes, or indexed by weight or length (Jackson, 1952; Jameson, 1950). Pregnancy can be determined at relatively early stages by the presence of embryos at autopsy. The occurrence of previous litters can be detected by placental scars, although the number of scars is a poor measure of the number of young previously produced (Davis _et al._, 1948; Corthum, 1967).

The use of such fatal measurements obviously limits other types of data that can be collected. No subsequent behavioral work can be done. Animals cannot be pre-tested to see if individuals with certain characteristics subsequently disperse. The conditions existing in control or residential populations cannot be monitored over extended periods while dispersal is being surveyed; the population is severely disturbed in the process of studying it. Finally, the fate that would have befallen dispersants cannot be determined.

Consequences and Functions

Natality, mortality, and dispersal ultimately control the levels of all animal populations (Mayr, 1970). Changes in gene frequencies in populations are accomplished through mutation, drift, selection, and dispersal (Smith, 1978). The ubiquity of dispersal attests to its importance; virtually every species of animal (and plant) has at least one dispersal stage in its life cycle.

The importance of dispersal is most vividly demonstrated by the consequences of its absence. Reproduction may be drastically reduced when populations are enclosed (Christian and LeMunyan, 1958; Crowcroft and Rowe, 1958; Lidicker, 1976; Lloyd and Christian, 1969; Terman, 1965; Vessey, 1967). Helmreich (1960) found an increase in intrauterine mortality under crowded laboratory conditions. Similarly, mortality of neonates and juveniles may increase in enclosed populations (Anderson, 1961; Brown, 1953; Lidicker, 1965, 1976; Louch, 1956; Southwick, 1955). Krebs *et al.* (1969) found that *Microtus* populations in large field enclosures rose to abnormally high densities and then crashed. Such results prompted Krebs *et al.* (1976, p. 79) to state that "...dispersal is necessary for normal population regulation in voles."

When emigration is possible, it may affect the source population in a number of ways. Crowcroft and Rowe (1958) found that after populations of *Mus musculus* in laboratory enclosures had ceased reproducing, providing access to an adjacent pen (allowing "dispersal") resulted in a resumption of reproduction. Similarly, Terman (1973) showed that non-reproductive members of asymptotic populations of *Peromyscus maniculatus* became reproductively active when removed from the population. Emigration directly removes individuals from a population and thus may slow the rate of growth of the source population. Lidicker (1975) discusses at length evidence for this from a number of sources for *Microtus californicus*. Mazurkiewicz (1972) found faster rates of growth in island populations of *Clethrionomys glareolus* than for adjacent mainland populations.

One population's emigrant is another population's immigrant and immigration can also affect populations. In extreme instances, excessive immigration may result in disruption of the population. The introduction of rats (*Rattus norvegicus*) to populations on city blocks resulted in the cessation of growth or actual decline in these populations; it was almost three months before breeding levels returned to normal (Calhoun, 1948; Davis and Christian, 1956). Ramsey and Briese (1971) found that an influx of immigrant *Sigmodon hispidus* resulted in the emigration of some residents (see also Terman, 1962). Immigration in any amount contributes directly to population size. McCarley (1959) found that immigration to an X-irradiated population was sufficient to keep the size of the population unchanged.

Evolutionary forces that favor dispersal have been suggested for populations. Lidicker (1962) stated that dispersal may function as a mechanism to keep population levels below the carrying capacity of the environment. Wilson (1975) noted that minimal dispersal can result in small effective population size and increased inbreeding, with a consequent loss of genetic variability. In addition, the species' range may be extended (Howard, 1965; Udvardy, 1969), and this may increase the stability and persistence of the species. The invoking of such factors for dispersal suggests group selection (e.g. Van Valen, 1971).

It is obvious from the foregoing discussion that dispersal can affect populations. I choose, however, to view the effects of dispersal on populations as secondary results. The functions of dispersal, in an evolutionary sense (Alcock, 1975), pertain to individuals, not populations. Dispersal is actually performed by individuals, and it is these individuals which ultimately reap the benefits or suffer the failure of the act. In this discussion, I will consider dispersal in terms of individual natural selection. Implicit in the idea of selection acting on individuals is the assumption that advantages accrue to dispersants, and these ultimately outweigh the disadvantages. Evolutionary arguments ultimately depend on differential reproduction.

One of the ways that a dispersant may benefit is by gaining opportunities for more and better matings. These include the "quantitative" and "qualitative" advantages proposed by Lidicker (1962, 1975). It may be that moving animals encounter more individuals, and thus more potential mates. It is necessary to extend this idea to recognize that the advantage may come in being able to breed at all. For instance, in _Mus musculus_ demes, there is typically a dominant male and several subordinate males; subordinate males are not reproductive (Anderson, 1970). Dispersal may allow an individual to establish his own territory and reproduce. Christian (1970) has hypothesized a major role in evolution to these dispersing subordinates. Under laboratory conditions, maturation and reproduction of females is delayed by exposure to their mother or littermates (Batzli _et al._, 1977; Cowley and Wise, 1972; Rogers and Beauchamp, 1976; Skryja, 1978). The role of these factors under natural conditions is unknown, but dispersal provides an escape from these effects if they occur.

Dispersal may allow an animal to mate with an individual from a different genetic background and thus produce novel, advantageous gene combinations. Such outbreeding promotes heterozygosity; Mayr (1970) and Smith (1978) have discussed the advantages of heterozygosity. This effect may be especially important to the founders of new populations (Mayr, 1970).

An animal may also benefit more indirectly from dispersal. In any environment, the host of factors that make a particular home range acceptable are constantly changing. Factors such as food, shelter, mates, and the number and intensity of social interactions are included. An animal may profit by moving to a new area if the overall sum of these factors sinks below some critical level (see Factors Initiating Dispersal, below). Such a response may allow an individual to avoid population crashes or improve the quality of its home range even if there is no crash. These advantages include what Lidicker called the "diplomatic" and "economic" benefits of dispersal.

While I have emphasized the advantages to individuals of dispersing, few data have been presented to substantiate the claim that these benefits actually occur. The ideas are logically and intuitively appealing, but demonstrations are rare. There are three basic reasons for this. First, in order to assess benefits directly accrued from mating, it must be known who mates with whom. This is virtually impossible to determine for small, secretive animals even in stable populations, not to mention an animal that merely passes through an area. Smith (1978) notes that dispersal should be viewed as a series of "copulation points" if its genetic effects are to be completely studied, but we know nothing of such points.

A second problem in assessing the advantages of dispersing is that the fate of animals emigrating (or disappearing) from study areas is often unknown (e.g. Michener and Michener, 1977). Similarly, a transient, observed momentarily in the act of dispersal, may either go on to genetic fame or oblivion. Thirdly, even if the fate of the dispersant is known, what would have happened had the animal not dispersed is unknown. Thus no relative benefit can be measured. As a final note, the difficulty of closely monitoring the fate of individuals compared to determining gross population characteristics may account in part for the popularity of viewing dispersal as a phenomenon of populations.

Besides considering the factors that favor dispersal, it is necessary to assess its hazards. In the laboratory, avian predation was higher on voles and mice moving in unfamiliar terrain than on individuals having prior experience in the enclosures (Ambrose, 1972; Metzgar, 1967). Errington (1963) found mink predation to be higher on transient than on resident muskrats. Carl (1971), studying arctic ground squirrels (Spermophilus undulatus) on a peninsula, found that animals unable to establish a territory in the main population lived as a group at the shoreline. This population was regularly flooded, and none of its occupants ever bred. Andrzejewski and Wroclawek (1961) have suggested that vagrant animals were more prone to die in live-traps.

Even if emigrants survive the visiccitudes of the wilderness, their immigration to an established population may be resisted by residents. The highest levels of aggression recorded by Armitage (1977) in yellow-bellied marmots occurred when immigrants attempted to enter the population. Barnett (1958) noted for rats that "the releasing stimulus most likely to lead to attack is the presence of a strange male of the same species" (see also Calhoun, 1948). Lidicker's (1976) attempts to introduce groups of house mice into occupied enclosures met with high aggression and failure (see also Flowerdew, 1974). Similarly, social interactions between strange Peromyscus leucopus are more aggressive than those between neighbors (Vestal and Hellack, 1978; see also Michener and Michener, 1973). Finally, animals introduced or immigrating to areas where residents have been removed remain longer than those on populated grids (Boonstra, 1978; Flowerdew, 1974; Redfield et al., 1978a,b).

Factors Initiating Dispersal

The forces that prompt an individual to disperse include both the characteristics of the environment and those of the individual. A great deal of attention has been placed on environmental factors (e.g. Fairbairn, 1978a), but the purpose of this section is not to exhaustively review these.

The major point to be recognized in this section is that the decision to disperse is mediated by environmental factors and the psychological make-up of the individual, and individuals vary in their responses to given environmental changes. In any environment there is a constellation of factors that determine the "acceptability" of a home range to an individual. These factors include the type and amount of food available and the effort required to procure it, the quantity and quality of refuges, the presence of potential mates, the threat of predation, the intensity of intra- and interspecific competition, the frequency and nature of social encounters, and undoubtedly many others. All of these factors vary in both time and space; therefore individuals must keep running tallies of the quality of their immediate surroundings. At any time the net total of all factors may sink below some critical level so as to make the home range unacceptable. This can be due to a drastic decline in one or two factors or a small decline in several aspects; other circumstances may even be good and improving.

Thus individuals are constantly choosing between alternatives (see King, 1977). If all is well, the choice is easily made: stay and pursue the strategies that are presently working. Dispersal is one of the options if conditions are unfavorable. This amounts to perceiving an area as unacceptable and being willing to try the same or different strategies in another location. Alternatively, an individual may stay and persist in its present strategies, or change its strategies; these constitute a revision of the criteria of acceptability.

Aggression, particularly its increase in growing or dense populations, is a popular explanation for dispersal. With some species, such as ground squirrels, aggression can be observed. Armitage (1977) and Carl (1971) attributed dispersal to aggression. Other authors, while observing aggression, have seen no relationship with dispersal (Bronson, 1964; Dunford, 1977; Slade and Balph, 1974; Yeaton, 1972). Aggression, as indexed by scarring, has been examined in more secretive species (e.g. Microtus: Christian, 1971; Rose and Gaines, 1976). Recruitment rates where residents have been reduced or removed have also been used to suggest a role for aggression in dispersal (Fairbairn, 1977; Flowerdew, 1974; Hansen and Batzli, 1978; Redfield et al., 1978a,b; Sadlier, 1965). Bekoff (1977) and King (1973) have questioned the relationship between aggression and dispersal, and suggested other social factors.

Resource shortages, particularly in food, have also been proposed as causes of dispersal (e.g. Fairbairn, 1978a). In Microtus, for example, high dispersal rates are associated with peak or rapidly increasing populations (Krebs et al., 1976; Myers and Krebs, 1971). Under very high-density conditions, the food supply may be visibly reduced; it has also been hypothesized that even before such devastation occurs, only low-quality food items may be available (Freeland, 1974). In general, however, it is not possible to know the quantity or quality of food available to a small mammal, not to mention what an individual perceives as being available to it. Some investigators have circumvented this problem by supplying supplemental food and examining changes in dispersal and recruitment. Strecker (1954) supplied the only food available to unconfined populations of Mus musculus. When food was supplied in abundance to one population, emigration was minimal; but when the amount of food available to another population was limited, emigration was higher, and the food supply was never exhausted. Hansen and Batzli (1978) found that supplemental food did not increase the density of *Peromyscus leucopus* in spring and summer.

Dispersal is certainly correlated with the onset of sexual maturation in a number of species (see Demographic Characteristics of Dispersants, below). It remains to be shown, however, whether the physiological changes associated with puberty cause dispersal or if puberty is correlated with other factors that actually prompt dispersal.

Howard (1960) proposed that for some individuals ("innate" dispersers) dispersal is independent of environmental factors. In these instances, the genotype of the animal is responsible. This hypothesis has yet to be confirmed (see Demographic Characteristics of Dispersants, below).

Given a complex of individuals, conditions, and potential responses as varied as that outlined above, individual variation will certainly exist. Individuals will differ in the conditions they deem acceptable and in their responses to a given set of environmental changes. In this light, the array of types and numbers of individuals dispersing is no surprise. Attempts to ascribe the majority of dispersal to one factor, especially when the level of other factors is uncontrolled or even unknown, seem foolhardy.

Demographic Characteristics of Dispersants

In the study of dispersal, knowledge of the characteristics of dispersants provides data which impart predictability to the phenomenon. In this section the age, sex, reproductive condition, and genetics of dispersing small mammals will be briefly reviewed.

One of the most common patterns seen is the movement, or at least the disappearance, of young individuals at about the time of sexual maturation; these individuals are presumably leaving the parental home range (Anderson, 1970; Bronson, 1964; Cameron, 1977; Christian, 1970; Davis _et al._, 1964; Dice and Howard, 1951; Dunford, 1977; Hansen and Batzli, 1978; Howard, 1949, 1960; Lidicker, 1975; Mazurkiewicz and Rajska, 1975; Michener and Michener, 1977; Myers, 1974; Petticrew and Sadlier, 1974; Rongstad, 1965; Slade and Balph, 1974; Smith, 1978; Wilson, 1975; Yeaton, 1972). This however, is by no means the only age at which dispersal occurs. King (1955) found that adult female prairie dogs may leave their burrows to their offspring and establish new homes on the edge of the colony (see also Jannett, 1978). In a number of studies, individuals of all age classes have invaded vacant areas or emigrated (Armitage, 1962, 1977; Briese and Smith, 1974; Delong, 1957; Fitch, 1948; Gentry, 1961; Joule and Cameron, 1975; Myers and Krebs, 1971; Pucek and Olszewski, 1971; Rowe _et al._, 1963; Stickel, 1946; Strecker, 1954; Tamarin, 1977; Van Vleck, 1968). In some studies, adults have predominated, at least in certain seasons (Kemp and Kieth, 1970; Lidicker, 1976; M'Closkey, 1972; Newsome, 1969; Rusch and Reeder, 1978).

Variation in the sex distribution of dispersants has also been found. Males and females may disperse in equal numbers (Joule and

Cameron, 1975; Strecker, 1954; Tamarin, 1977; Van Vleck, 1968). In some instances, females outnumber males (Myers, 1974; Myers and Krebs, 1971; Smith, 1978; Tamarin, 1977). However, it is more common for males to outnumber females (Bronson, 1964; Fairbairn, 1978a; Krebs *et al.*, 1976; Lidicker, 1976; Michener and Michener, 1977; Rongstad, 1965; Rowe *et al.*, 1963; Slade and Balph, 1974; Stickel, 1946; Yeaton, 1972).

Dispersants are often non-reproductive, either because of their age, their social subordination, or both. However, a number of exceptions are noteworthy. Tast (1966) found that some female *Microtus oeconomus* moved from uplands to the lowlands in the spring while pregnant (see also Jannett, 1978). Some sexually mature *Microtus pennsylvanicus* and *M. ochrogaster* invaded depopulated areas (Myers and Krebs, 1971). Tamarin (1977) found immigrant voles to be more reproductive that residents. In *Mus musculus*, Strecker (1954) reported that 42 of 44 females leaving the population had perforate vaginas and 12 of 44 were pregnant (see also Newsome, 1969; Rowe *et al.*, 1953). Harland *et al.* (1978) mention dispersal by pregnant female *Peromyscus leucopus*; Fairbairn (1977) found that *Peromyscus maniculatus* in colonization areas were as reproductively active as residents from a control plot.

The genetics of dispersing animals is important because of the hypothesized role of genes in initiating dispersal (Howard, 1960) and the effects of dispersal on the genetics of populations (Smith, 1978). Howard (1960) proposed that a class of individuals ("innate" dispersers) exists in which the occurrence and extent of dispersal is determined primarily by the genotype. This hypothesis has yet to be verified, but genetic differences between residents and immigrants have been found at specific loci. Myers and Krebs (1971) reported on differences between resident and immigrant *Microtus pennsylvanicus* and *M. ochrogaster* at the transferrin and leucine aminopeptidase loci. Differences in the frequencies of leucine aminopeptidase alleles have similarly been described for *Microtus townsendii* (Krebs *et al.*, 1976). In house mice (*Mus musculus*), Lidicker (1976) found disproportionate representation of albinos among animals emigrating from enclosures; but dispersing feral house mice did not differ at two loci (Myers, 1974). In *Spermophilus richardsonii* there were no differences at the transferrin locus between residents and animals entering or lost from the population (Michener and Michener, 1977).

Some of these data lend support to Howard's ideas, but the precise relationship, if any, between these genes and dispersal is unknown. The loci examined are limited to the structural genes that can be assayed electrophoretically (and show some variation in the population being studied). Smith (1978) addressed the problems associated with a locus-by-locus approach, and instead favors examining overall heterozygosity.

Behavioral Characteristics of Dispersants

There are two major reasons to expect that dispersants differ behaviorally from residents. First, residents and dispersants are distinguished on the basis of behavior. The latter leave their home ranges and attempt to establish new ones, whereas residents are relatively sedentary. In defining dispersal in terms of such a complex behavior, it is easy to assume that concomitant behavioral differences exist. Second, behavioral change is one of the fastest ways that an individual can respond to a change in environmental conditions (Wilson, 1975). Dispersants may possess a constellation of characters that increase their likelihood of dispersing and enable them to cope more easily with the different and changing environments encountered. Alternatively, dispersants may develop this constellation of characters as a result of dispersing and becoming established.

There are three reasons why it would be advantageous to discover behavioral differences between residents and dispersants. First, such factors may provide information on the causes of dispersal. Second, behaviors might be found that increase the chances of a dispersant surviving. Third, the factors responsible for the differences could be examined.

The results of tests for behavioral differences between residents and immigrants have so far been limited. Halpin and Sullivan (1978) found that individuals from island populations of _Peromyscus maniculatus_ were less aggressive than those from the mainland; they attributed the difference to the frustration of dispersal on islands. These results are only obliquely applicable to the problem at hand because they deal with behavioral changes over evolutionary time spans. In the laboratory, avian predation was higher on mice and voles moving in unfamiliar terrain than on those with prior experience in the enclosures (Ambrose, 1972; Metzgar, 1967). The parallel with residents and immigrants under natural conditions is obvious, but the specific behavioral differences associated with this differential mortality are unknown. Vestal and Hellack (1978) showed that encounters between strangers were more aggressive than those between neighbors in *Peromyscus leucopus*. Again, parallels with dispersal are present, but the difference seemed to be related to the prior establishmant of dominance. Actual immigrants were not tested.

Myers and Krebs (1971) compared the behavior of resident and immigrant *Microtus pennsylvanicus* and *M. ochrogaster* in the laboratory. There were no clear differences in aggressiveness or general activity, although *M. pennsylvanicus* immigrants tended to be more aggressive when field population were at peak densities. Dispersing males of both species showed less exploratory behavior in a maze than residents. Fairbairn (1978b) performed similar tests on resident and immigrant *Peromyscus maniculatus*. Dispersing males were less exploratory and less aggressive than resident males, but were generally more active.

Barriers and Dispersal

Barriers, by definition, inhibit the movements of animals. This is obvious in the instances of such massive topographical features as mountains, deserts, and large bodies of water (Udvardy, 1969). However, the role of local, seemingly small, habitat discontinuities is not so clear.

All environments are, to some extent, heterogeneous. Dispersing individuals may face a choice of crossing or not crossing habitat in which they would not normally reside. Barriers such as streams, roads, fields (to a woodland form), and forest (to a grassland form) are crossable by all healthy, normal members of a population; but they are actually crossed by only some members. These environmental features act as barriers by limiting the type of individual that will choose to cross.

In comparing animals that disperse across barriers with those which disperse within continuous habitat and those which do not disperse at all, the first necessary step is to examine the demographic and behavioral characteristics of these groups. Dispersal across habitat not normally occupied by the species is the type most likely to result in the founding of new populations, expansion of the species' range, and gene flow between local populations. In addition, these animals remove themselves from the source population and may affect density regulation. The risks associated with this frontier-crossing are also reasonably assumed to be greater. Factors which may increase a dispersing individual's chances of surviving and reproducing would be most evident in this group. Movements within patches of continuous habitat pose lesser gains, but also lesser risks. Information on the characteristics of animals which undertake these types of movements can also serve as a basis for subsequent hypotheses and tests regarding the causes and effects of such dispersal.

There is evidence that local topographical features such as roads produce some effects on the movements of small mammals. Studies of <u>Rattus</u> <u>norvegicus</u> in urban areas have shown that rats rarely move between city blocks (Davis and Christian, 1956; Emlen <u>et</u> <u>al.</u>, 1948). This effect is so pronounced that when block-populations were completely erradicated, it was two years before the areas were re-populated to the carrying capacity of the environment (Emlen <u>et</u> <u>al.</u>, 1948). Similarly, streets kept an albino group of pocket gophers (<u>Thomomys</u> <u>umbrinus</u>) isolated from normally-colored groups (MacClaughlin, cited in Udvardy, 1969). When both sides of roads in forested areas were monitored using live-traps, Oxley <u>et</u> <u>al.</u> (1974)

found that woodland small mammals (*Peromyscus leucopus*, *Tamias striatus*, and *Sciurus carolinensis*) seldom crossed roadways wider than 20 m. Roads and 15 m-wide mown strips have likewise been shown to inhibit the movements of *Sigmodon hispidus* and *Reithrodontomys fulvescens* (Cameron, 1977; Joule and Cameron, 1975). Note that these habitat discontinuities can be crossed in seconds and could be crossed by any member of the population; yet most individuals do not cross.

Bodies of water may pose more substantial barriers to the dispersal of terrestrial animals. Beer *et al.* (1954) found the islands of a large lake to be populated only by non-hibernators. They concluded colonization of the islands was possible only across the ice in winter. However, even crossing the ice requires travelling long distances in barren, hostile habitat. Christianson (1977) documented the occasional crossing of a frozen lake by *Peromyscus*. Sheppe (1965) found that *Peromyscus leucopus* will disperse by swimming; ten mice swam 100-410 ft between islands. A tidal flat prevented *Microtus californicus* from colonizing an island for some time (Lidicker and Anderson, 1962); once some voles had crossed, they populated the island and the population of house mice already on the island became extinct (Lidicker, 1966).

The effects of habitat discontinuities on homing have also been examined. Savidge (1973) found evidence that a stream (3-4 m wide) decreased the homing performance of *Peromyscus leucopus*. Contrary to this, *Peromyscus leucopus* transported across powerline corridors homed as well as conspecifics displaced an equal distance into the forest (Schreiber and Graves, 1977); The authors note that the mice seldom cross the corridors on their own. It should be noted that a test of homing does not address the question of whether or not an individual would have voluntarily dispersed across the barrier.

In each of the above studies, no reports are made of attempts to distinguish those individuals which disperse across barriers from those which disperse within continuous habitat. The central question of the differences between these two groups has yet to be addressed.

CHAPTER 2

DEMOGRAPHIC CHARACTERISTICS OF PEROMYSCUS LEUCOPUS DISPERSING WITHIN AND BETWEEN WOODLOTS

The goal of this experiment was to determine if, and if so how, *Peromyscus leucopus* which disperse across habitat discontinuities differ demographically from conspecifics which invade a vacant area within continuous habitat. In addition, each of these groups was compared to the resident population. The variables examined were sex, age, and reproductive condition. The *a priori* hypotheses were that mice dispersing between woodlots would be younger and less reproductively active than those dispersing within a woodlot; the sex distributions of the two immigrant groups were not expected to differ.

Methods and Materials

Two types of experimental plots were established: "isolated" and "contiguous". There were four plots of each type. Isolated plots were small woodlots which were separated from the nearest woodlot by at least 100 m of agricultural field or pasture. No continuous, wooded fence rows connected isolated woodlots to any other forested area. Therefore *P. leucopus* could only reach isolated plots by crossing habitat they would not regularly inhabit. Grids of traps completely covered these isolated woodlots. Table 1 lists, for all woodlots, the size, distance to the nearest woodlot, and surrounding habitat. Figure 1 is an aerial photograph showing most of the study area.

One contiguous plot was established for each isolated plot. Each was equal in size to an isolated plot and located in the center of a woodlot at least three times as large as the corresponding isolated plot. Contiguous plots were shaped as near to square as possible, considering the number of trap stations needed to cover the appropriate area. Mice could disperse onto contiguous plots while remaining in wooded habitat; immigration onto contiguous plots from other woodlots was probably minimal due to the relatively long distances to neighboring woodlots (Table 1). Figure 2 shows the conditions for each treatment diagramatically. All plots were located on or near the campus of Michigan State University, East Lansing, Michigan. The vegetation of all plots was mature deciduous forest; prominent species of trees included maple, beech, oak, and ash.

Each plot was snap-trapped for 28 consecutive days. This length of time provides a sufficiently large sample, makes the experiment easily replicable, and does not, I feel, impose an exceedingly severe drain on the source populations for the contiguous plots. The trap interval was 15.2 m (50 ft); there was one trap per station. The bait was a mixture of peanut butter and cotton; this mixture reduces predation by slugs and insects when compared to straight peanut butter (Getz and Prather, 1975). Traps were checked each morning.

P. leucopus captured during the first seven days of trapping were considered residents, and those captured thereafter termed immigrants.

Table 1. Description of the study plots.

Plot	Dates Used	Size of woodlot (ha)	Distance to Nearest Woodlot (m)	Habitat Surrounding Woodlot
1-I	June 1976 Sept. 1976 June 1977 Sept. 1977	0.41	110	Grazed pasture
1-C	June 1976 Sept. 1976 June 1977 Sept. 1977	5.20	640	
2-I	June 1976 Sept. 1976 June 1977 Sept. 1977	0.75	270	Alfalfa Tall-grass field Vegetable garden
2-C	June 1976 Sept. 1976 June 1977 Sept. 1977	6.35	450	
3-I	June 1976 June 1977	1.51	100	Alfalfa Grazed pasture Short-grass field
3-C	June 1976 June 1977	5.81	400	
4-I	Sept. 1976 Sept. 1977	0.47	120	Tall-grass field Corn
4-C	Sept. 1976 Sept. 1977	5.00	580	

Figure 1. Aerial photograph of the study area.

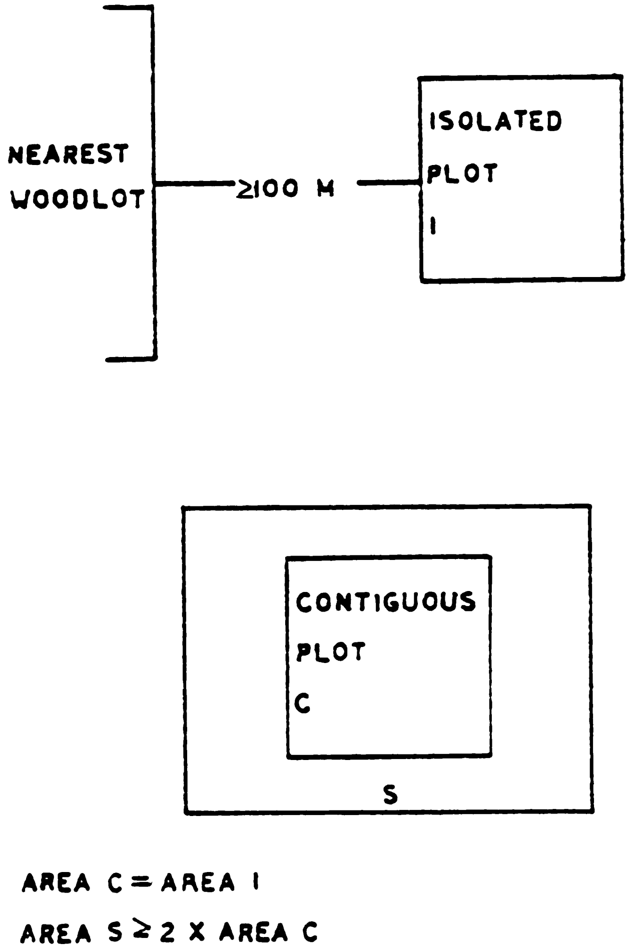

Figure 2. Schematic representation of the requirements for the experimental conditions. Area "S" is the untrapped portion of a woodlot which contains a contiguous plot.

Thus there are three treatment groups: "isolated immigrants", "contiguous immigrants", and "residents". In some analyses (see the description of the analysis, below), isolated and contiguous immigrants were pooled; these two groups together are called "immigrants".

Pilot studies were undertaken in the year prior to the start of the main experiments to test the validity of distinguishing residents and immigrants. One isolated and one contiguous plot were used in both August and October (these were plots 2-I and 3-C for the main experiment). Each plot was live-trapped for three days prior to the start of 25 days of snap-trapping. All P. leucopus live-trapped were marked and released. Twenty-two of 31 marked mice (71%) were subsequently snap-trapped. In three of the four plot-trapping periods unmarked mice were caught on or before the day when the last marked mice were caught. Conversely, several marked mice were caught relatively late in the trapping period. These results cast some doubt on the possibility of making an iron-clad distinction between residents and immigrants. It is quite possible that some immigrants are present from the first day of removal trapping, and, conversely, a small proportion of residents might be caught later when mostly immigrants were being captured.

Several alternative methods for distinguishing residents and immigrants were considered, and it was concluded that, no matter what procedure was used, the status of some mice would always be questionable. Thus the criterion of capture on or before the seventh day was adopted. It is acceptable for five reasons. First, of the 22 marked mice that were snap-trapped, 18 were caught by the seventh day. This indicates that by that time most, if not all, residents have been removed. Second, the rate of capture of all mice declined to very low levels by the seventh day and did not change appreciably thereafter. This suggests that only immigrants are present after that time. Third, inclusion of residents in the immigrant groups would produce a conservative estimate of any difference between the immigrant groups and between residents and immigrants, because preliminary analysis showed no substantial differences between residents from various plots. Fourth, misclassification of immigrants as residents, while resulting in the loss of some data on immigrants, would not affect the primary comparison, i.e. that of the two immigrant groups. Fifth, this procedure is easily replicable.

The experiments were conducted in June and September of 1976 and 1977; thus there were four trapping periods. Three isolated and three contiguous plots were used in each trapping period; the trapping schedule for each plot is given in Table 1. For each trapping period, at least one pair of plots that had not been used for a minimum of one year was trapped. This provided some control for the effects of prior trapping.

The dependent variables examined were sex, age, and reproductive condition. Animals were autopsied immediately after the traps were checked.

Age can be estimated in a number of ways (for a review see Pucek and Lowe, 1975). Two methods were used here. First, to examine age class distribution, animals were classified as "adults" or "juveniles". The rational for this distinction is to indicate what proportions of the treatment groups are of sufficient age to breed. Juveniles weighed less than 15.0 g and were shorter than 150 mm total length; adults exceeded one or both of these criteria. Seventy-two P. leucopus from the pilot studies were assigned to these age classes by me on the basis of size, pelage, and condition of the external genitalia. Sixty-nine of these mice (95.8%) conformed to the above criteria when subsequently weighed and measured. The requirements for these age classes are in agreement with those used by other investigators (Bendell, 1959; Fairbairn, 1977, 1978a; Jackson, 1952).

Besides determining age on the discrete basis of whether or not an animal has achieved some criterion (e.g. sufficient size to breed), age may also be measured as a continuous variable which provides finer resolution than the age classes previously established (i.e. adult/juvenile). The weight of the dried eye lens has been shown to be one of the most useful indicators of age in mammals in general (Pucek and Lowe, 1975), and specifically, in P. leucopus. For 71 P. leucopus of known age (18-148 days), Millar and Iverson (1976) found the weight of the eye lens to be linearly related to the log of age ($r = 0.982$). Data on eye lens weight was collected in September, 1976 and in June and September, 1977.

In order to determine eye lens weight, both whole eyeballs were removed at autopsy and fixed for a minimum of two weeks in 10% formalin. The lens was then removed from one randomly chosen eye, cleaned, dried for three days at 75° C, and weighed (± 0.05 mg). From the time of removal from the oven until weighing, the lenses were kept in a covered vessel with a desiccant (anhydrous $CaSO_4$) to avoid weight increase from absorption of atmospheric moisture. Preliminary tests with Peromyscus eremicus, a species similar in body size to P. leucopus, showed that lens weight did not decrease with extended drying after three days; the weight of the first several lenses weighed had not increased when they were reweighed at the end of a session.

Male reproductive condition was indexed by the weight of the right testis (± 5.0 mg). Some mice were infested with botfly larvae (Cuterebra sp.) in both fall trapping periods. These larvae occur in the inguinal or scrotal area (see Whitaker, 1968). Infestation can affect the weight (Smith, 1977) and position (Wecker, 1962) of the testes, as well as sterilize the host (Dalmat, 1942). Therefore all infested males were excluded from the analysis of male reproductive condition.

Females were classified as being pregnant, having placental scars, or being non-reproductive (having neither embryos nor placental scars). Two additional measures were obtained from pregnant females. First, the number of embryos was recorded as an estimate of potential litter size. Second, for each litter, the crown-rump length of a randomly chosen embryo was measured (± 0.5 mm)as an index to the stage of pregnancy. For both males and females, only adults were considered in the analysis of reproductive condition.

The discrete variables of sex, age class distribution, and female reproductive condition were analyzed using X^2 contingency tables (see Gill, 1978, for a discussion of the use of multi-way X^2 tests). The continuous variables were eye lens weight, male reproductive condition, litter size and embryo length. Each of these was analyzed using cross-classified analysis of variance (AOV). Specific contrasts within each AOV were done using Scheffe's Test (Gill, 1978). For each of these contrasts, the primary comparison was that of isolated immigrants to contiguous immigrants. If these groups were significantly different ($P < .05$), then each was compared to the residents. If they were not different, they were pooled as immigrants and compared to residents.

For all analyses, data on immigrants to the three plots in each treatment were pooled for each trapping period. Data for residents on all six plots were likewise pooled. Although this results in the loss of information on interplot variability, inclusion of this factor would have excessively reduced the sample sizes in some instances. Any variability between plots is still present; it is just not explicitly expressed.

Results

Table 2 lists the sex, age, and reproductive condition of residents, isolated immigrants, and contiguous immigrants according to plot and trapping period. A total of 529 *Peromyscus leucopus* were captured.

The distribution of the sexes was initially analyzed in a 4-way contingency table; the factors were sex, treatment group (i.e. isolated immigrant, contiguous immigrant, and resident), season, and year. The null hypothesis was that the distribution of males and females is independent of the other factors. The results of this test were statistically significant ($P < .005$), therefore the seasons were analyzed separately. The 3-way tests of sex, treatment group and year produced significant results for both June ($P < .005$) and September ($P < .005$). Ultimately, then. a 2-way test (sex x treatment group) was done for each trapping period. For each there was no significant difference between isolated immigrants, contiguous immigrants, and residents in the distribution of males and females (June 1976: X^2 = 1.070, $P > .50$; Sept. 1976: X^2 = 0.770, $P > .50$; June 1977: X^2 = 2.751, $P > .10$; Sept. 1977: X^2 = 5.379, $P > .05$; for each: df = 2). These data are shown in Figure 3. When isolated and contiguous immigrants were pooled, the sex distribution of immigrants did not differ from that of the residents in any trapping period (for each: $P > .10$).

As with sex, the distribution of adults and juveniles was initially analyzed in a 4-way contingency table, with the factors being age class, treatment group, season, and year. The results of this test were statistically significant ($P < .005$), therefore the seasons were analyzed separately. The 3-way tests of age class, treatment group, and season produced significant results for both June ($P < .005$) and September ($P < .005$). Therefore a 2-way test (age class x treatment group) was done for each trapping period. For each there was no significant difference between isolated immigrants, contiguous immigrants, and residents (June 1976: X^2 = 1.486, $P > .10$; Sept. 1976: X^2 = 2.608, $P > .10$; June 1977: X^2 = 1.108, $P > .50$; Sept. 1977: X^2 = 3.736, $P > .10$; for each: df = 2). These data are shown in Figure 4. Similarly, immigrants did not differ from residents in any trapping period ($P > .10$).

The independent variables in the analysis of eye lens weight were treatment group, year, season, and age class. There was a significant interaction of treatment group and age class ($P = .008$), so adults and juveniles were analyzed separately. There were no significant effects of seasons or years so these factors were pooled.

For adults, isolated immigrants had significantly smaller lenses than contiguous immigrants ($f = 20.775$; df = 2, 209; $P < .005$). Adult contiguous immigrants were statistically the same as adult residents ($P > .25$); and adult isolated immigrants were significantly younger than residents ($f = 33.513$; df = 2, 209; $P < .001$). The data for each trapping period are shown in Figure 5. When pooled over years and seasons, the mean ± 1 s.e. eye lens weights for adults were: 67.16 ± 2.81 for isolated immigrants, 84.30 ± 2.51 for contiguous immigrants, and 88.70 ± 2.36 for residents. Within the juvenile age class, there were no significant differences between treatment groups, juvenile isolated immigrants did not differ from contiguous immigrants ($P > .75$), and immigrants were the same as residents ($P > .25$). For all juveniles, the mean ± 1 s.e. eye lens weight was 48.63 ± 1.41 ($n = 64$).

In the analysis of male reproductive condition (testis weight), there was a significant interaction of treatment group, season, and year ($P = .016$), so each trapping period was analyzed separately. In June 1976, isolated immigrants were the same as residents ($P > .75$); and contiguous immigrants were significantly less reproductive than these two groups ($f = 16.072$; df = 2, 75; $P < .001$). In June 1977 all three groups were highly reproductive and did not differ from each other (for both: P .75). In both Septembers the immigrant groups did not differ (for both: $P > .75$); but immigrants were less reproductively active than residents (1976: $f = 17.552$; df = 2, 37; 1977: $f = 24.393$; df = 2, 23; for both: $P < .001$). The data are shown in Figure 6.

The data for female reproductive condition were pooled across seasons and years because the low numbers of adult females captured in some trapping periods precluded reliable non-parametric analysis. Therefore a single test of reproductive condition (pregnant, placental scars, non-reproductive) by treatment group was performed. The result of the test showed that the treatment groups differed significantly ($X^2 = 13.695$; df = 4; $P < .01$). The major contributions to this X^2 value came from a lack of pregnant females and a surplus of non-reproductive females among contiguous immigrants, relative to the other groups. This indicates that, overall, adult female isolated immigrants and residents were equally reproductive, and more so than contiguous immigrants. Figure 7 shows the reproductive condition of adult females in each treatment group for each trapping period.

Litter size of the pregnant females was analyzed in terms of treatment group, year and season. There was a significant effect of treatment group ($f = 3.567$; df = 2, 63; $P = .034$); no other primary effects or interactions were significant. The analysis of the treatment groups, pooled over seasons and years, showed that isolated immigrants were not different from contiguous immigrants ($P > .75$), but immigrants as a group had significantly smaller litters than residents ($f = 6.747$: df = 2, 71; $P < .05$). The data are shown in Figure 8a.

In the analysis of embryo length, treatment group, season, and year were the independent variables. Neither any interactions nor any primary effects were significant (for the effect of treatment group: $P = .173$). There was, however, an obvious trend for isolated immigrants to be in an earlier stage of pregnancy than contiguous immigrants or residents (Figure 8b).

Table 2. Demographic data for each plot for each trapping period.

	Ad-Juv		♂-♀		Lens wt. x (mg x 10) s.e.;n		Testis wt. x (g) s.e.;n		Preg-Ps-Nr	
	Res	Im	Res	Im	Res	Im	Res	Im	Res	Im
June '76										
1-I	11-6	5-1	7-10	5-1	-	-	.10 .03;3	(0)	6-0-1	3-0-2
2-I	20-11	4-3	15-16	5-2	-	-	.17 .03;8	.11 .06;3	6-2-4	0-1-0
3-I	9-8	8-2	6-10	4-6	-	-	.22 .04;3	.21 .06;3	1-4-1	3-4-1
1-C	11-1	10-3	5-7	8-5	-	-	.17 .04;4	.15 .04;7	4-1-2	2-0-1
2-C	15-9	13-9	12-12	10-12	-	-	.14 .04;6	.08 .02;8	3-3-3	1-3-1
3-C	30-11	29-5	25-16	20-14	-	-	.14 .02;16	.05 .01;17	7-2-5	0-4-8
Sept '76										
1-I	11-2	8-0	6-7	4-4	76.7 6.4;11	63.5 5.7;8	.09 .08;2	.02 .01;4	2-3-1	1-0-3
2-I	3-1	5-2	2-2	4-3	67.0 15.0;2	66.6 9.3;5	.19 .00;1	.01 .00;3	1-0-1	0-1-1
4-I	12-7	8-5	10-9	7-6	105.2 7.1;11	79.4 7.1;8	.11 .05;5	.04 .03;3	1-2-1	0-1-2
1-C	17-1	22-9	11-7	18-13	83.4 3.4;16	89.9 4.8;21	.12 .05;6	.01 .00;11	1-3-2	0-3-5
2-C	16-0	8-4	4-10	6-6	90.9 4.9;11	102.6 4.4;8	.07 .06;2	.01 .00;1	4-6-0	0-4-0
4-C	4-2	1-0	3-3	1-0	82.0 13.6;4	89.5 16.5;2	.14 .00;1	.09 .00;1	2-0-1	0-0-0

Table 2 (cont'd).

	Ad-Juv		♂-♀		Lens wt. $\bar{x}$ (mg x 10) s.e.;n		Testis wt. $\bar{x}$ (g) s.e.;n		Preg-Ps-Nr	
	Res	Im	Res	Im	Res	Im	Res	Im	Res	Im
June '77										
1-I	2-0	5-2	0-2	5-2	101.0	57.6	(0)	.13	2-0-0	2-0-0
					14.0;2	4.3;5		.04;3		
2-I	2-0	1-0	2-0	1-0	63.5	55.0	.09	.13	0-0-0	0-0-0
					5.5;2	0.0;1	.03;2	.00;1		
3-I	2-1	3-1	1-2	3-1	67.5	57.0	.08	.13	1-0-0	1-0-0
					6.5;2	4.5;3	.00;1	.04;2		
1-C	1-0	2-0	1-0	1-1	(0)	90.7	(0)	.19	0-0-0	1-0-0
						17.8;3		.00;1		
2-C	2-0	7-3	1-1	7-3	65.5	82.9	.19	.18	1-0-0	1-1-0
					6.5;2	8.5;7	.00;1	.02;5		
3-C	5-1	12-0	2-4	6-6	78.6	66.1	.19	.10	2-2-0	5-0-1
					12.7;5	6.1;12	.00;1	.03;6		
Sept '77										
1-I	2-0	1-0	1-1	1-0	81.0	94.0	.26	(0)	0-1-0	0-0-0
					10.0;2	0.0;1	.00;1			
2-I	5-4	3-1	4-5	4-0	102.0	71.3	.24	.04	2-2-0	0-0-0
					0.0;1	11.9;3	.00;1	.01;2		
4-I	1-0	3-0	0-1	2-1	80.0	68.0	(0)	.10	0-1-0	1-0-0
					0.0;1	3.4;3		.00;1		
1-C	4-0	8-2	1-3	6-4	76.8	70.1	(0)	.13	1-1-1	2-0-1
					8.8;4	3.7;8		.04;4		
2-C	3-0	3-0	1-2	2-1	94.0	73.0	(0)	.08	2-0-0	1-0-0
					1.5;3	7.8;3		.00;1		
4-C	11-3	22-6	7-7	20-18	112.9	88.6	.21	.03	2-2-0	0-2-8
					6.3;11	5.5;20	.02;6	.01;10		

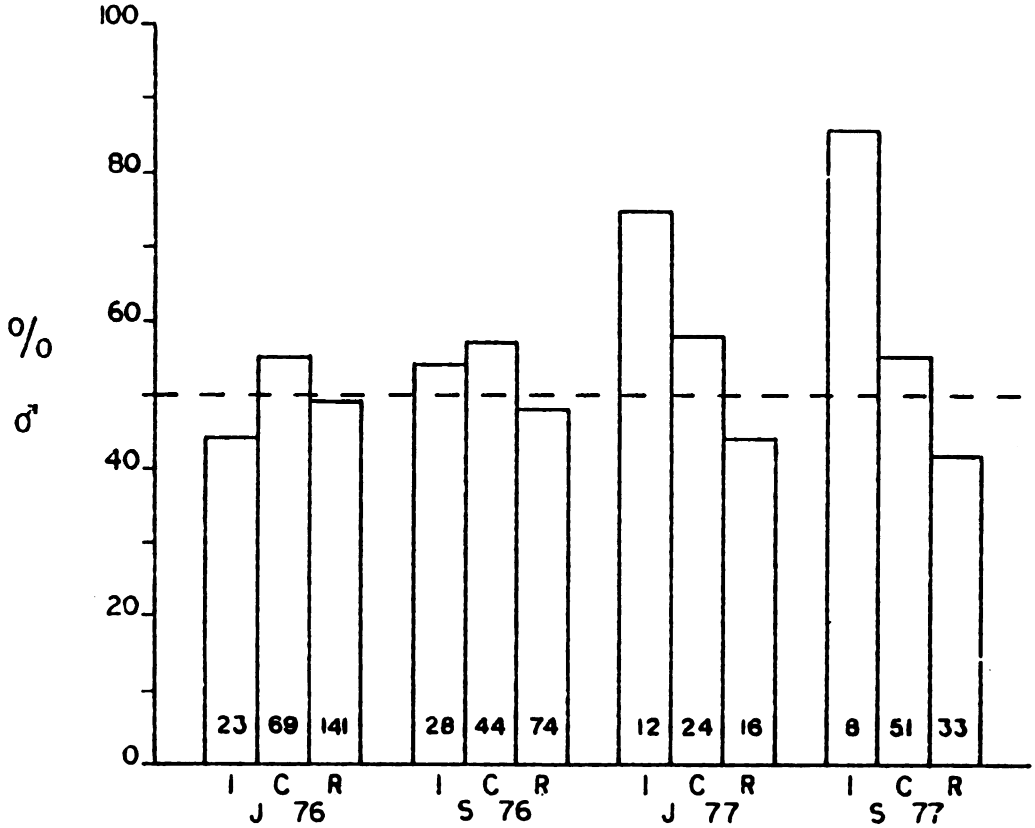

Figure 3. Distribution of males and females.

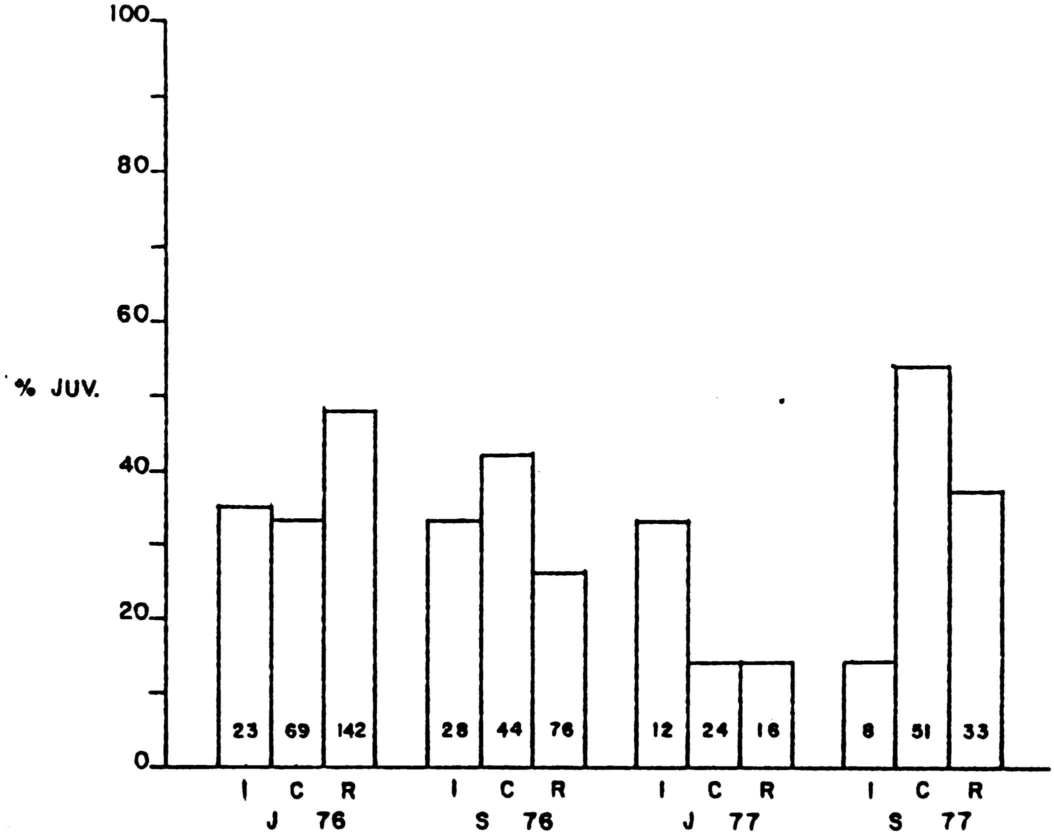

Figure 4. Distribution of adults and juveniles.

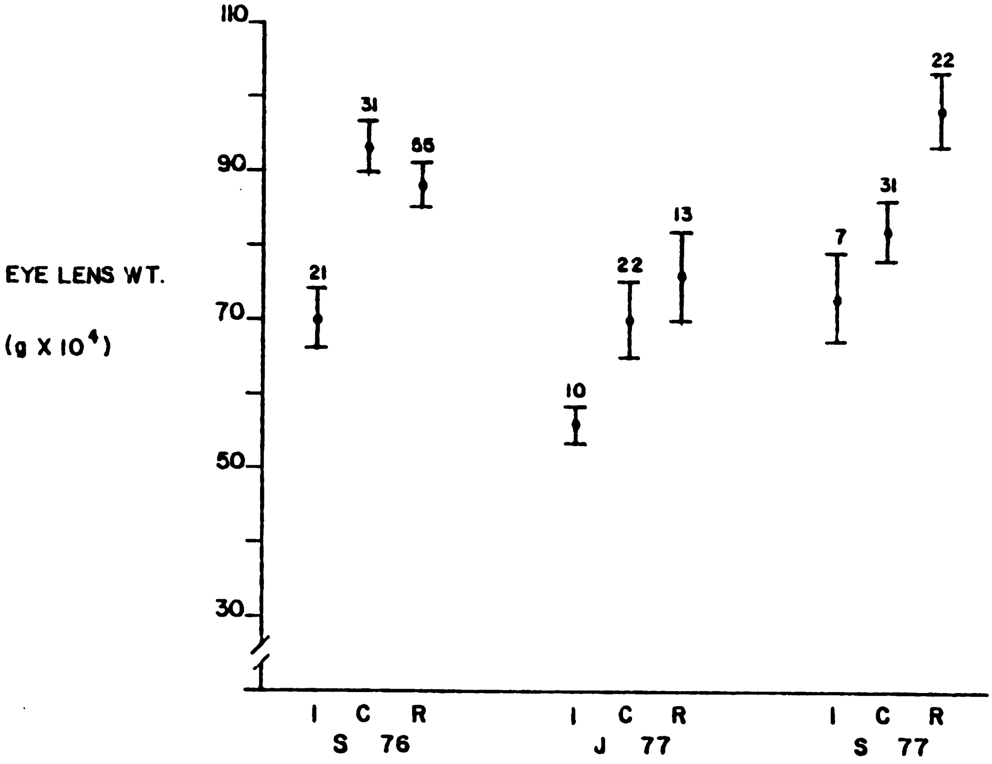

Figure 5. Mean ± 1 s.e. eye lens weight for adults.

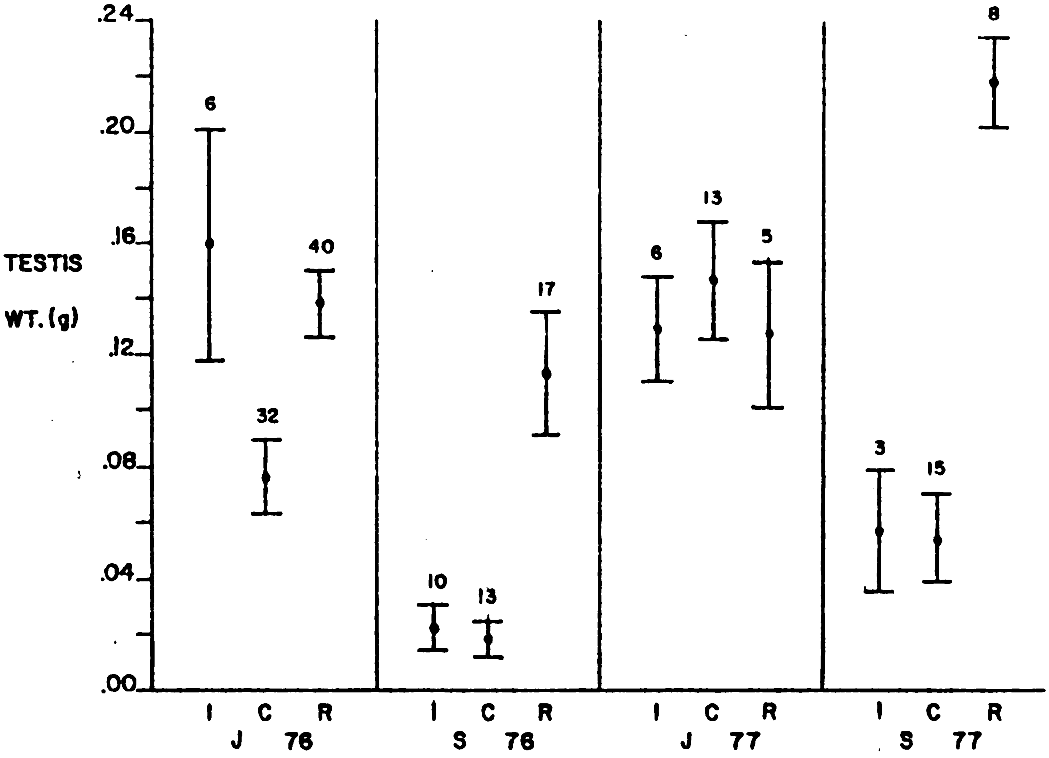

Figure 6. Mean + 1 s.e. testis weight for adult males.

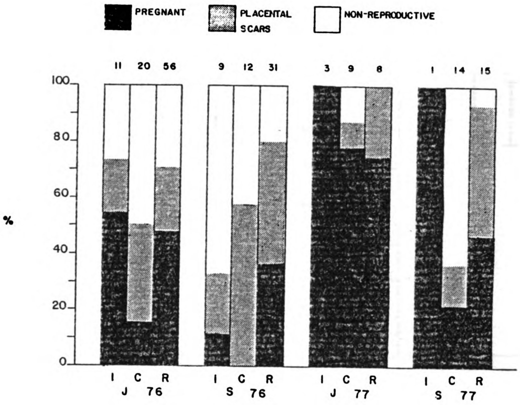

Figure 7. Percentage of adult females in each reproductive condition.

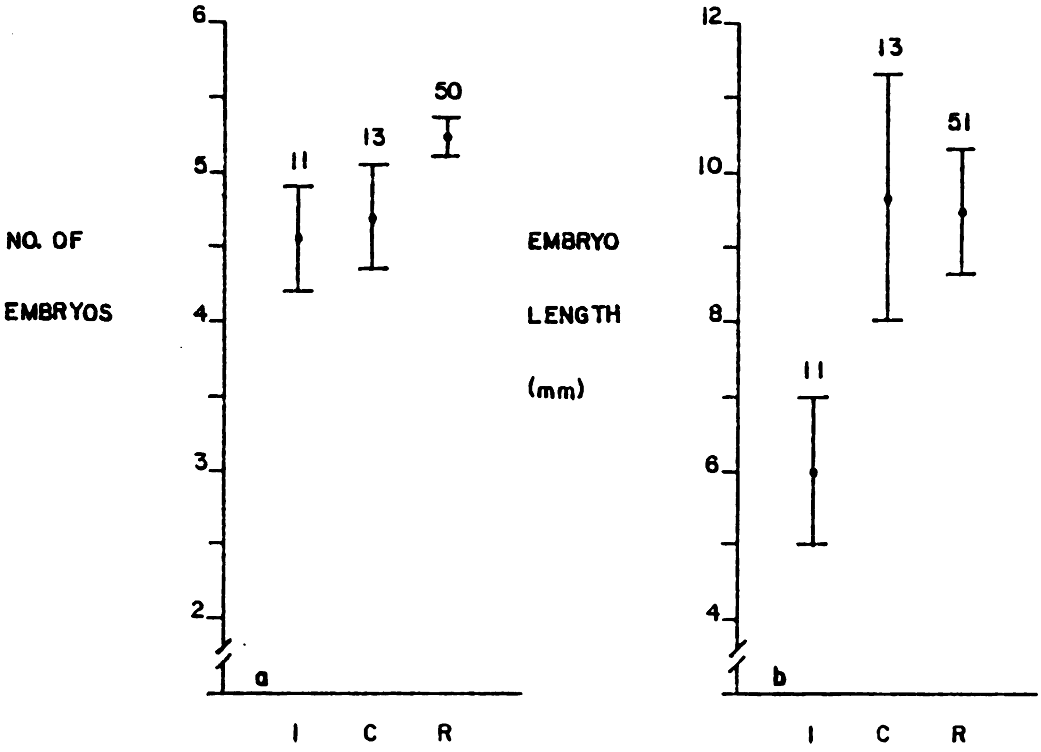

Figure 8. Mean + 1 s.e. (a) litter size and (b) embryo length for pregnant females.

Discussion and Conclusions

For each trapping period, the sex distributions of isolated immigrants, contiguous immigrants, and residents were not significantly different. The significance of the three- and four-dimensional X^2 tests indicates the presence of variation between trapping periods, and this variation is obvious in Figure 3. Three points should be noted. First, both the contiguous immigrants and residents show relatively little seasonal and yearly variation in sex ratios. The percentage of males ranged from 42-50% and 55-58% for the two groups, respectively. Second, for each trapping period, the sex ratio of the contiguous immigrants is slightly higher than that of the residents, regardless of their absolute value. Third, isolated immigrants show the most seasonal and yearly variation (range: 44-88% males).

The relatively high and variable percentage of males among isolated immigrants might be the result of differential movement by the sexes. The two highest ratios (in June and September, 1977) occurred at the times of the lowest resident densities, but there is no evidence to suggest that this would affect the sex ratio of barrier-crossers. Alternatively, the predominance of males in these two periods may be due to the vagaries of small sample sizes. The highest percentages were found in the smallest samples. Also, live-trapping for isolated immigrants in October, 1976 and September, 1978 produced about equal numbers of males and females in equally small samples. This evidence leads to the tentative conclusion that the habitat discontinuities had no effect on the sex distribution of the immigrants.

No differences were observed between isolated immigrants, contiguous immigrants, and residents in the proportions of the groups that were adults, i.e. animals that were of sufficient age to breed. There is some variation between trapping periods, but no consistent patterns are evident. Although the two immigrant groups did not differ, these results nevertheless provide interesting and valuable information. The majority of residents were adults, as might be expected. Similarly, contiguous immigrants were generally adult. Some adults would be expected if resident animals were moving in from peripheral areas to fill vacancies, but the preponderance of animals of breeding age strongly suggests that dispersal is not primarily undertaken by juveniles. This conclusion is borne out by the age class distribution of the isolated immigrants; two-third or more of them were of adult size in each trapping period. Their status as adults is reinforced by the fact that, in both spring trapping periods, most isolated immigrants judged to be of adult age were reproductively active (Figures 6 and 7). These results indicate that P. leucopus disperse predominantly after the age of puberty.

Overall, adult female isolated immigrants were significantly more reproductive than adult contiguous immigrants. Pooling over seasons and years, while a statistical necessity, does not reveal the variation between trapping periods. Thus, while an overall effect is seen, conclusions regarding these data must be restricted. In general, the level of reproductive activity in females paralleled that in males (see Figures 6 and 7). An exception can be seen in the data from isolated immigrants in September, 1977, where adult males were reproductively inactive, but the single adult female was pregnant. In general, then, males and females in each group were equivalently reproductive, and the discussion following from the results in males also applies to females.

In general, reproductive activity did not serve to discriminate the two immigrant groups. Isolated and contiguous immigrants differed significantly only in June 1976, when the former were highly reproductive (like residents) and contiguous immigrants were reproductively inactive. In June 1977 all three groups were reproductively active. In both September trapping periods, the immigrants were alike and significantly less reproductive than residents. Possible causes of the differences seen and the consequences of dispersal of highly reproductive mice to small, isolated patches of habitat will be deferred until the General Discussion.

Age, as measured by eye lens weight, was the only variable that consistently differed between the two immigrant groups. For each trapping period, adult isolated immigrants were significantly younger than adult contiguous immigrants. Contiguous immigrants were statistically the same as residents. Although the age classes were analyzed separately to localize any differences, the relationships between treatment groups do not change substantially when adults and juveniles are considered together. Within each trapping period, a graded sequence can be seen. At one extreme are the oldest animals, the residents; at the other extreme are the isolated immigrants -- the youngest group in each instance. Between these two groups are the contiguous immigrants.

The results of the analysis of eye lens weight are consistent with the hypothesis put forward in the introduction. Namely, mice dispersing across barriers would be predominantly young animals, whereas older mice would be expected to fill vacancies in continuous habitat.

In summary, besides differing in the behavioral variable of crossing or not crossing barriers, isolated immigrants are significantly younger than contiguous immigrants. The two immigrant groups did not consistently differ in sex, age class distribution, or reproductive condition. Because isolated and contiguous immigrants were initially defined according to a behavioral difference in the field, the question arises as to whether the two groups can be further distinguished by independent tests of behavior in the laboratory. The next chapter deals with behavioral tests for differences between isolated and contiguous immigrants.

CHAPTER 3

BEHAVIOR OF ISOLATED IMMIGRANTS, CONTIGUOUS IMMIGRANTS AND RESIDENTS

Introduction

The characteristic used to distinguish isolated and contiguous immigrants in the field was their crossing of a barrier imposed by at least 100 m of habitat not usually occupied by *P. leucopus*. It was also possible to separate the two types of immigrants by age, since isolated immigrants had smaller eye lens weights than contiguous immigrants. If crossing a barrier in nature is a reliable behavioral characteristic that differentiates between types of immigrants, and is not an isolated act or a chance occurrence, then independent, controlled behavioral tests in the laboratory should confirm the behavioral difference observed in the field.

Experiment 3.1

Barrier Crossing

Barriers to movement in the laboratory may have little resemblance to those in the field, but it is possible that isolated immigrants are more inclined to enter strange and somewhat noxious habitat. Such conditions can be presented in the laboratory. The hypothesis tested here was that isolated immigrants will cross a water barrier and drop into a strange situation in greater numbers than contiguous immigrants and residents.

Methods and Materials

In order to obtain members of the three treatment groups, grids 2-I and 2-C (Table 1) were live-trapped for seven consecutive days, then two days per week for five weeks. Trapping began on 6 September 1978. As in the field experiment (Chapter 2), residents were captured in the first week, and immigrants were caught thereafter. Thus residents came from both grids, grid 2-I supplied isolated immigrants, and grid 2-C supplied contiguous immigrants. All mice were removed upon first capture.

The mice were tested 7-13 days after capture. Females with litters or in the advanced stages of pregnancy were not tested. Between capture and testing, mice were housed individually in a room with other mice to be tested. Wood shavings, cotton nesting material, and *ad lib* food were provided. During the first five days in captivity, water was provided on a restricted schedule as described in Experiment 3.2; thereafter it was provided *ad lib*. The photoperiod in the colony approximated that of nature for that time of year (September).

The test apparatus is shown in Figure 9. The home and finish cages were outfitted like the cages in which the animals were kept in the colony (27.5 x 12.5 x 15.0 cm). In the water barrier, the water was approximately 7.5 cm deep; a fiberboard lid prevented travel along the cage top. Thus it was necessary for mice to swim in order to cross. The drop barrier was a 51 cm length of 10 cm diameter translucent PVC pipe with fiberboard top and bottom. Once a mouse jumped down, it could not return to the home cage. The design of the apparatus was such that a mouse could not see any of the lower shelf until after it had jumped. Each home cage was visually isolated from others by pieces of sheet metal. Tunnels were made of hardware cloth. The photoperiod was synchronous with that of the colony and the natural photoperiod; a dim red light was provided during the dark period.

Mice were put into the apparatus at about 1200 hr, with the tunnel connecting the home cage and the water barrier blocked. On the next day (c. 1200 hr) the block was removed, giving the mice access to the remainder of the apparatus. This allowed one dark period for acclimation to the home cage prior to testing. Mice were checked the following morning to determine whether or not they had moved to the finish cage. Preliminary studies with other P. leucopus showed that mice that did not cross on the first night of availability did not cross on subsequent nights, and those which crossed on the first night would cross on subsequent nights if returned to the home cage.

The data were analyzed using a X^2 contingency test.

Results

The treatment groups differed significantly ($X^2 = 6.820$; $P < .05$). This was due to frequent crossing by isolated immigrants and limited crossing by both the contiguous immigrants and residents, which were similar in the percentage of mice crossing (Table 3).

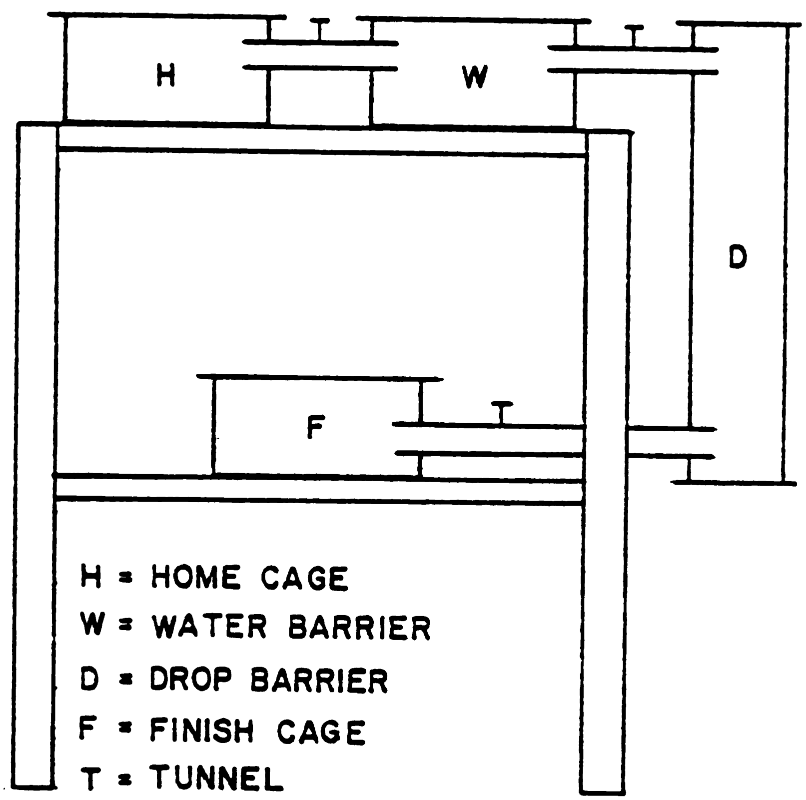

Figure 9. Diagram of the barrier apparatus (lateral view).

Table 3. Performance of the treatment groups in the barrier apparatus

Treatment Group	% Crossing	n
Isolated Immigrants	87.5	7
Contiguous Immigrants	30.0	10
Residents	31.3	16

Experiment 3.2

Neophobia

The hypothesis tested in this experiment was that isolated immigrants will show less neophobia toward a novel fluid than contiguous immigrants, and both of these groups will exhibit less neophobia than residents.

Methods and Materials

The isolated and contiguous immigrants used in the barrier test (Experiment 3.1) were also used in this experiment. Residents were procured by live-trapping grid 1-C from 4-11 October 1978. As before, all mice were removed upon first capture.

The mice were provided with water for 24 hr immediately following capture. Water was supplied in two 10 cc drinking tubes. *P. leucopus* generally drink less than 5 ml per day, so a surplus of water was provided. On days 2, 3, and 4 after capture, mice were again given two tubes with water, but only for the two hours immediately following the onset of darkness. Mice were tested on day 5. The drinking tubes used for both training and testing were those designed by Robbins (1977).

As noted in the previous experiment, wood shavings, cotton nesting material, and _ad lib_ food were provided. The photoperiod in the colony room was similar to that in nature at the time. All measurements were made in the home cage. Females nursing litters or in the advanced stages of pregnancy were not tested.

For testing, the mice were again given two drinking tubes for the two hours following the onset of darkness, but a 20% sucrose solution (weight/volume) was given in the most preferred position. The other tube contained water as usual. The most preferred position was the one from which the greatest amount of fluid had been drunk over days 2-4; putting the sucrose in this position helped insure that the mice contacted the novel fluid. The mice's use of the drinking tubes on days 1-4 insured that only the fluid was novel during the test. The deprivation administered prior to testing guaranteed that the mice would drink measurable amounts during the test period, but the test night was not the first time that the mice were deprived. Increased consumption could have been obtained by exposing the mice to the fluids for a longer time, but an excessive decline in novelty might have occurred. A 20% sucrose solution was chosen because _Peromyscus maniculatus_, given this situation, drink about 50% of their total consumption from the sugar-water (R. Robbins, pers. comm.); thus either diminished or enhanced neophobia can be demonstrated. The simultaneous use of water and sugar-water provides a very sensitive test because the mice were not forced to drink something novel or go thirsty while under deprivation.

Neophobia was quantified as the proportion of sucrose solution in the total consumption during the test (sugar-water/sugar-water + water). The use of proportions may bias variance because the limits of the response are fixed; a $\sin^{-1}\sqrt{x}$ transformation of the raw data was performed to avoid such a bias (Bishop, 1966; Schefler, 1969). The transformed data were analyzed using a one-way analysis of variance.

Results

There were significant differences among the treatment groups ($f = 5.202$; $df = 2, 32$; $P < .025$). Residents and contiguous immigrants were equally neophobic, and more neophobic than isolated immigrants. The untransformed data are shown in Table 4.

Table 4. Neophobia of the wild-caught mice.

Treatment Group	Mean % ± 1 s.e.	n
Isolated Immigrants	64.7 ± 4.7	9
Contiguous Immigrants	44.9 ± 5.0	15
Residents	42.5 ± 4.5	11

Experiment 3.3

Feeding Diversity

The prediction of this experiment was that isolated immigrants will have more diverse feeding preferences than contiguous immigrants, and both of these groups will exhibit more feeding diversity than residents. This experiment has been published as Tardif and Gray (1978).

Methods and Materials

Following the snap-trapping in September 1976, grids 1-I, 2-I, 1-C, and 2-C (Table 1) were left undisturbed for two weeks and then live-trapped twice weekly for five weeks to provide isolated and contiguous immigrants. Residents were obtained by live-trapping a previously unmanipulated woodlot once weekly during the first three weeks of live-trapping on the grids listed above. All mice were removed upon first capture. Animals were housed individually for two weeks prior to testing. Wood shavings, cotton nesting material, and *ad lib* food and water were provided.

Mice were tested in the colony room in large plastic cages (20 x 48 x 38 cm), each having a central nest box, cotton nesting material, *ad lib* water, and four food dishes (6 cm diameter). Four foods were used: raw, shelled peanuts; shelled sunflower seeds; millet; and wheat germ. These foods were chosen because they were conveniently available and differed widely in such properties as size, shape, and texture.

Consumption of each food was measured (± 0.1 g) daily for six days; hoarded and scattered food was recovered and not counted as eaten. Each food dish contained the same food throughout the test and was randomly assigned to one of the corners of the cage daily. Because the mice eat about 2.5 g of food per day, refilling of each dish to 5.0 ± 0.2 g each day prevented forced generalization. This technique was developed by Gray (1977).

Diversity was calculated using the Shannon Index, H' (Pielou, 1975; Shannon and Weaver, 1964), where $H' = -\sum p_i \log_e p_i$; p_i = percentage of total food consumption of the i^{th} food type, n = total number of food types. For this experiment, $n = 4$. Diversity is lowest (feeding is most specialized) when an animal eats one food exclusively ($H' = 0$). When consumption is divided equally between the four categories, diversity is highest, and feeding is most generalized ($H' = 1.386$).

Several measures of diversity can be calculated given the three-dimensional structure of the data, which includes foods, days, and individuals. Two measures of diversity are used here. The first, diversity within days ($\overline{H'}_w$), is computed by determining a diversity value for each day for each animal (H'_w), then computing a mean for each animal based on six days. This is a measure of an animal's average daily diversity for six foraging bouts (nights). Mean diversity within days for a treatment group is denoted by $\overline{\overline{H'}}_w$ This was chosen _a priori_ as the primary index of specialization or generalization because it is based on individual nights and thus represents the finest possible partitioning of the animal's behavior.

The second measure, diversity over days (H'_o), is calculated by summing the raw data for a given animal over the six days and computing one H' for each animal from these four sums. This is a measure of an animal's diversity over the total test period. By summing over days, daily changes in preferred foods can raise the estimate of diversity over days while diversity within days remains constant; hence, H'_o is a "noisier" measure of diversity than $\bar{\bar{H}}'_w$.

Because $\bar{H}'_w$ is a mean, tests for differences between the treatment groups can be analyzed parametrically; Student's t-test was used. Tests of H'_o used the Mann-Whitney U-statistic. The value of $\bar{H}'_w$ for one contiguous immigrant was a statistical outlier, and none of his data were used. Sample sizes for analysis were nine residents, 10 contiguous immigrants, and eight isolated immigrants.

Results

Figure 10A shows the data for $\bar{\bar{H}}'_w$; all trends are in the predicted direction. Contiguous immigrants were not significantly different from isolated immigrants ($t = 0.418$; $df = 16$; $P > .25$, one-tailed). However, immigrants showed significantly higher diversity within days than residents ($t = 1.849$; $df = 25$; $P < .05$, one-tailed). There were no significant differences between the groups in H'_o (contiguous immigrants versus isolated immigrants: $U = 41$, $P > .10$; residents versus immigrants: $U = 99$, $P > .10$) (Figure 10B).

Discussion and Conclusions

The behavioral characteristics of *P. leucopus* vary according to whether they have dispersed within continuous habitat or across habitat discontinuities. Isolated immigrants cross barriers in greater numbers and are less neophobic than contiguous immigrants. The two immigrant groups do not differ significantly in feeding diversity, although isolated immigrants tend to be slightly more

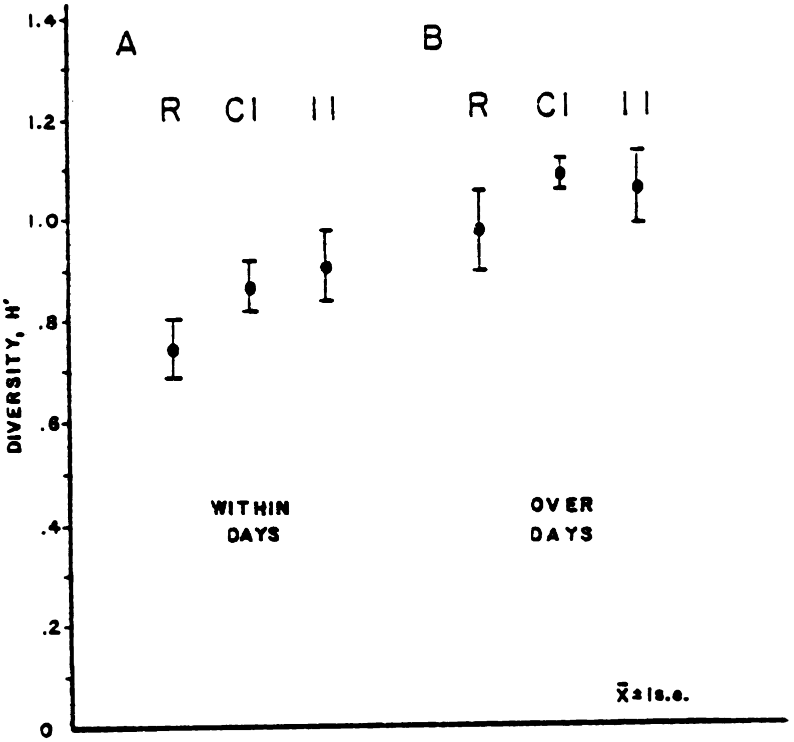

Figure 10. Mean ± 1 s.e. feeding diversity. A) $\overline{H'}_w$; B) H'_o.

diverse; immigrants as a group have more diverse preferences than residents.

In each of the three experiments the differences between the three groups are in the predicted directions. At one extreme, residents are the least likely to cross barriers, the most neophobic, and the most specialized feeders. At the other extreme, mice which have dispersed across habitat discontinuities are the most likely to cross laboratory barriers, the least neophobic, and the most generalized feeders. In each instance, immigrants from within continuous habitat show intermediate values of the behaviors. In the tests of barrier crossing and neophobia, they are essentially the same as residents; their feeding diversity is like that of the isolated immigrants, but slightly lower.

The results of the barrier experiment strongly reinforce the assertion that the two immigrant groups are qualitatively different in correlation with their differential dispersal. The barrier test was not designed to duplicate dispersal in the laboratory. Rather, it was an attempt to construct a "filter" -- an apparatus through which some, but not all, mice would choose to move. Fourteen of 33 mice (42%) crossed the barriers, indicating that some selection was occurring. The fact that much of the selection occurred according to the hypothesized variable indicates that the distinction between within-woodlot and between-woodlot dispersants is meaningful.

The results of the test of neophobia are straightforward and require little additional explanation. Isolated immigrants are less reluctant to try a novel fluid than contiguous immigrants and residents. Such a behavioral characteristic would seem to be beneficial to an individual attempting to become established in a new patch of habitat. Contiguous immigrants are only slightly less neophobic than residents; this would be expected from their movement to invade a vacant area with the limitation of their movement to being within a woodlot.

The results of the test of feeding diversity are more complex. On a daily basis, immigrant P. leucopus show significantly more diverse feeding preferences than residents. These findings are consistent with the hypothesis that unpredictable environments are populated by generalists. Note, however, that it is familiarity with the environment that is different between the groups. Predictability is a function of the animals' knowledge of their environment; it does not depend on changes in the food supply.

A significant difference was found between immigrants and residents in diversity within days, but not diversity over days. This means that over the total test period the groups ate from the food categories in approximately the same proportions; the difference lies in how these proportions were reached. Immigrants sampled approximately equal amounts of the four foods each night; residents ate predominantly one or two foods each night, but changed preferred foods from night to night. We might speculate that the food supply in the different woodlots is somewhat similar and that, given enough time, conspecifics would deplete these resources in similar proportions. That is we would predict that diversities of comsumption in the field, summed over several days, would be similar; but because of the predictability of the food supply, resident and immigrants should differ in their daily strategies to accomplish this. Also, given similar nutritional needs and identical foods in this test, one would expect that the mice's diets would be similar when summed over a sufficiently long period of time.

The design of the behavioral experiments tends to produce a conservative estimate of any differences seen between the groups. There are three reasons for this. First, by removing animals for the resident group at first capture, it is likely that recent immigrants and imminent emigrants would be included in the group. Known immigrants are more likely to cross laboratory barriers, are less neophobic, and exhibit higher feeding diversity; inclusion of them in the resident group would raise the value for that group. Similarly, if animals possess these characteristics prior to dispersal, including animals that are about to disperse would raise the resident's value. Second, although the chances are small, the contiguous immigrants might contain immigrants that had dispersed between woodlots. Their inclusion would tend to minimize differences between the immigrant groups. Finally, the very existence of the differences after the animals were removed to the laboratory and tested under contrived conditions argues for the presence of strong initial differences.

Isolated and contiguous immigrants differ behaviorally, but the causes of these differences are unknown. Chapter 4 will describe investigations of possible origins of the differences seen here.

CHAPTER 4

THE DEVELOPMENT OF BARRIER CROSSING, NEOPHOBIA AND FEEDING DIVERSITY

Introduction

The causes of the behavioral differences observed in the laboratory may be age, experience, genetics, or some combination. Since genetic manipulation would require extended breeding procedures, I chose to examine the effects of age on barrier crossing and the effects of age and experience on neophobia and feeding diversity. If the manipulation of these variables produces behavioral differences similar to those obtained for isolated immigrants, contiguous immigrants and residents, then the differences might be attributable to these ontogenetic factors.

Experiment 4.1

The Effect of Age on Barrier Crossing

In Experiment 3.1 isolated immigrants crossed the barriers in the laboratory apparatus in significantly greater numbers than contiguous immigrants and residents. In the demographic study (Chapter 2), isolated immigrants were found to be younger than contiguous immigrants and residents. The specificity of behaviors often increases with age (Balaban, 1975; Bateson, 1976; Gibson, 1969; Lehrman and Rosenblatt, 1971). Therefore, the effect of age on performance in the barrier apparatus was tested.

Methods and Materials

All P. leucopus used were the F_1 offspring of the animals live-trapped in the fall of 1978 (see Experiment 3.1). Each was housed individually after weaning at 21 days of age. The mice used in this experiment were also used in the tests of the development of neophobia (Experiment 4.2).

There were two treatment groups: 1) "young" mice were tested in the barrier apparatus at 46-51 days of age; 2) "old" mice were tested at 90-93 days of age. Different mice were used in each group.

The apparatus was the same as that used to test wild-caught mice in Experiment 3.1 (see Figure 9). The testing procedure was also the same. Mice were put in the home cage on day one and restricted there. On day 2 the tunnel between the home cage and the water barrier was unblocked. On day 3 data were recorded; mice either remained in the home cage or moved to the finish cage.

The performance of the groups was compared using a X^2 contingency table.

Results

There was no significant effect of age on the number of animals which crossed the barriers ($X^2 = 0.203$; df = 1; $P > .50$). In the young group, 5 of 32 mice (16%) crossed; in the old group, 6 of 30 mice (20%) crossed. There was no difference between males and females ($X^2 = 0.067$; df = 1; $P > .50$).

Experiment 4.2

The Development of Neophobia

Isolated immigrants were less neophobic than both contiguous immigrants and residents (Experiment 3.2). This difference might be attributable to age because isolated immigrants were younger than contiguous immigrants (Chapter 2), and behavior often becomes more specific with age (see references in Experiment 4.1). The observed differences among wild-caught mice might also be attributable to experience. The neophobia of laboratory rats is decreased after experience with novel flavors (Braveman and Jarvis, 1978; Capretta *et al.*, 1975; Siegel, 1974; Tarpy and McIntosh, 1977). In addition, if experience influences neophobia, then the effect could either be relatively enduring, or could diminish with time after the experience. In this experiment the effects of age, prior experience, and amount of time between experience and testing were investigated with laboratory-reared *P. leucopus*.

Methods and Materials

The *P. leucopus* used were the F_1 offspring of the mice captured in the autumn of 1978 (see Experiment 3.1). The mice went on to be tested in the barrier apparatus (Experiment 4.1) after this experiment.

Two variables were manipulated: experience with novel fluids and the amount of time between experience and testing. There were four treatment combinations; members of a litter were randomly assigned to one of these at weaning.

Experience was either "limited" or "diverse". All mice received this training from 21-40 days of age. The limited experience group received only water during rearing. Water was presented to them in drinking tubes when their counterparts in the diverse groups received the flavors (see below). Thus each group had equal experience with the drinking tubes prior to testing. Diverse experience consisted of being exposed to five differently flavored solutions: 1) sour (0.75 ml of 37% HCl in 500 ml H_2O); 2) salty (5.85 g NaCl in 1000 ml H_2O); 3) bitter (3.0 grains quinine sulfate in 400 ml H_2O); 4) coffee (2.5 g instant, decaffeinated coffee in 500 ml H_2O); 5) lemon (2.5 ml lemon juice in 500 ml H_2O). It had previously been determined that mice could detect these flavors at these concentrations, and would drink them (Robbins, 1977). Note that no sweet flavors were present, so there can be no generalization of flavors from experience to testing. Mice in the diverse groups received each flavor for three days (24 hr access) with one day of water between each flavor. Water was administered in drip-type bottles, standardly used in the colony. The sequence of flavors was randomly determined, but the same for all mice that were weaned on the same day. Therefore, the mice that entered training on the same day received the same random ordering of the flavors, but mice that started on different days had different random sequences. All flavors were presented alone to insure experience with them. The drinking tubes were refilled daily; approximately 10 cc of fluid were provided each day -- about twice the amount that the mice usually drink.

The mice were trained from 21-40 days of age. The "immediate" group was tested with sucrose at 44 days. The "delayed" group was tested at 88 days. Members of the delayed groups were housed individually and given *ad lib* water in colony water bottles between training and testing.

Thus the four treatment combinations were "limited-immediate", "diverse-immediate", "limited-delayed", and "diverse-delayed". Comparison of the limited-immediate and diverse-immediate groups provides a test of the effect of experience. A comparison of the limited-immediate versus limited-delayed groups tests the effect of age. The relationship between the limited and diverse groups when testing was immediate versus delayed shows the effect of the delay.

The test procedure was the same as that used for the wild-caught animals in Experiment 3.2. That is, mice were given access to two drinking tubes containing water for two hours per night for three consecutive nights. On the fourth night, a 20% sucrose solution was presented in the most preferred position; the other tube contained water; and again, access was provided for two hours. All work was done in the two hours immediately following the onset of darkness in the colony room.

There were sixteen mice in each treatment combination. Analysis was done using a two-way analysis of variance (AOV) to test for overall differences. Specific contrasts were done using Bonferroni t-tests (Gill, 1978). As in Experiment 3.2, the test statistic was the proportion of total consumption of the sucrose solution, and the data were subject to a $\sin^{-1}\sqrt{x}$ transformation prior to analysis.

Results

The AOV showed no significant overall effect of either experience ($f = 3.123$; $P > .05$) or delay in testing ($f = 1.072$; $P > .25$). However, within the immediate group, mice with diverse experience were significantly less neophobic than those with limited experience ($t_B = 2.65$; $P < .025$). In the delayed group, the neophobia of the limited group decreased somewhat, and that of the diverse group increased somewhat. Among mice with limited experience the difference between immediate and delayed testing was not significant ($t_B = 1.472$; $P > .05$). Similarly, the neophobia of mice with diverse experience did not significantly increase ($t_B = 1.300$; $P > .05$). Nonetheless, the limited and diverse groups were almost identical when testing was delayed. There was no difference between males and females ($t = 1.455$; $df = 62$; $P > .10$). The untransformed data are shown in Table 5.

Table 5. Mean ± 1 s.e. percentage of sugar-water consumption

	Immediate	Delayed
Limited	42.96 ± 4.05	50.89 ± 3.90
Diverse	57.16 ± 4.03	50.23 ± 3.39

Experiment 4.3

The Development of Feeding Diversity

Wild-caught isolated and contiguous immigrants were significantly more diverse in their feeding preferences than residents (Experiment 3.3). Experience was considered as a possible cause for this difference. Preliminary data suggested that wild-caught *P. leucopus* were more diverse in their feeding than F_1 laboratory-reared mice. The genetics of the two groups is similar, but their experiences are quite different. The *a priori* hypothesis of this experiment was that mice exposed to a fluctuating, unpredictable diet would show more diverse feeding preferences than those having experience with stable diets. The initial prediction of a difference among the wild-caught groups was based on this premise (see Introduction), and the results of Experiment 3.3 are consistent with this hypothesis.

As with the other developmental experiments, age was considered as a possible factor in the difference between the wild-caught residents and immigrants, because of the age differences observed among the treatment groups in the demographic study (Chapter 2). Therefore, the hypothesis that young *P. leucopus* are more generalized feeders than old mice was also tested. This work is being published as Gray and Tardif (in press).

Methods and Materials

The mice were the F_1 offspring of the *P. leucopus* live-trapped in the fall of 1976 (see Experiment 3.3). They were weaned at 21 days of age, and one third of each litter was assigned randomly to each group.

Three treatment groups were established to test for the effects of experience: "Fluctuating", "Stable", and "Choice" with 18 mice in each group. These mice were reared on four foods that mice will eat: brazil nuts, shredded coconut, oatmeal and sesame seeds (with the exception of the Choice group, explained below). During treatment, mice were housed singly in the colony room. Each day the prescribed diet was given to the mice in a metal dish (45 mm deep x 82 mm diameter). The next day any uneaten food was removed and new food was put into the dish. *Ad lib* water and cotton nesting material were provided. Supplemental feedings of approximately 0.4 g of lab chow per day were given to the few mice that looked sick and to the Fluctuating group on days when their random numbers were low (explained below). The treatment continued for a total of 69 days, until the mice were tested at 90 days of age.

The Fluctuating group received one of the four foods in a different amount each day. The type of food was chosen randomly. The amount (± 0.05 g) was determined by a number selected randomly from a normal distribution with a mean of 2.5 and a standard deviation of 1.5. This mean was chosen because the previous study (Experiment 3.3) showed that adult *P. leucopus* eat about 2.5 g of food per day. The standard deviation was selected to give widely fluctuating amounts without starving the mice. All mice in this group were fed the same on any day; thus mice weaned at different times received slightly different random treatments.

The Stable group received a constant diet of 0.7 ± 0.05 g of each of the four foods daily (2.8 g total). Thus the diets of the Stable and Fluctuating groups were similar if summed over a long period of time. What differed was the pattern in which the foods were presented; one was predictable, the other was not.

The Choice group was first tested for feeding diversity immediately after weaning (the "Juvenile" group, below). They then received a constant diet of approximately 2.8 g of each of the treatment foods daily (11.2 g total). These animals had a similar choice, only with different foods, in the six-day test and in treatment; I assumed that experience with the test foods from days 21-27 did not affect their feeding diversity at 90 days of age. Note that the Choice group, like the Stable group, had a predictable diet; unlike the Stable group, they were not forced to sample widely from the four foods each day.

In addition to the three treatment groups, two additional groups were used to test for the effects of age. The "Juvenile" group ($n = 18$) was tested for feeding diversity immediately after weaning. The "Adult" group ($n = 17$) was reared from weaning to testing (at 90-150 days of age) on ad lib laboratory chow.

The procedure for testing feeding diversity and methods of analysis were the same as in Experiment 3.3. Mice received 5.0 g each of peanuts, sunflower seeds, millet and wheat germ for six days; consumption was monitored daily. Diversity was measured as $\overline{H}'_w$ (average daily diversity for an individual over the test period). This measurement was used because it showed the difference between wild-caught residents and immigrants. Data were analyzed using Student's t-test.

Results

The data support the hypothesis that experience with a fluctuating diet increases feeding diversity. The Stable and Choice groups did not differ in diversity ($t = 1.15$; $df = 32$; $P > .20$), and the Fluctuating group was significantly more diverse than these two pooled groups ($t = 2.61$; $df = 47$; $P < .01$).

Age did not affect feeding diversity. The Juvenile and Adult groups did not differ significantly ($t = 0.42$; $df = 33$; $P > .50$). Also, males did not differ from females ($P > .10$).

The feeding diversity of the groups is shown in Figure 11.

Three mice from the Fluctuating group and one each from the Stable and Choice groups died during treatment. The numbers are not significantly different from an equal probability of death regardless of treatment ($X^2 = 1.6$; $P > .30$). Most of the mice grew well on the diets and all appeared healthy at testing.

Discussion and Conclusions

P. leucopus at about the age of puberty did not differ from older adults in their frequency of crossing the barrier apparatus. The conclusion follows that the difference seen in the comparison of isolated immigrants versus contiguous immigrants and residents (Experiment 3.1) probably cannot be attributed to age.

In view of the importance of experience in the development of neophobia and feeding diversity, it is easy to speculate that the differences observed in the wild-caught mice in the barrier test were due to differences in experience. This idea is reinforced by the fact that 18% of the lab-reared mice (11 of 62) crossed the barriers,

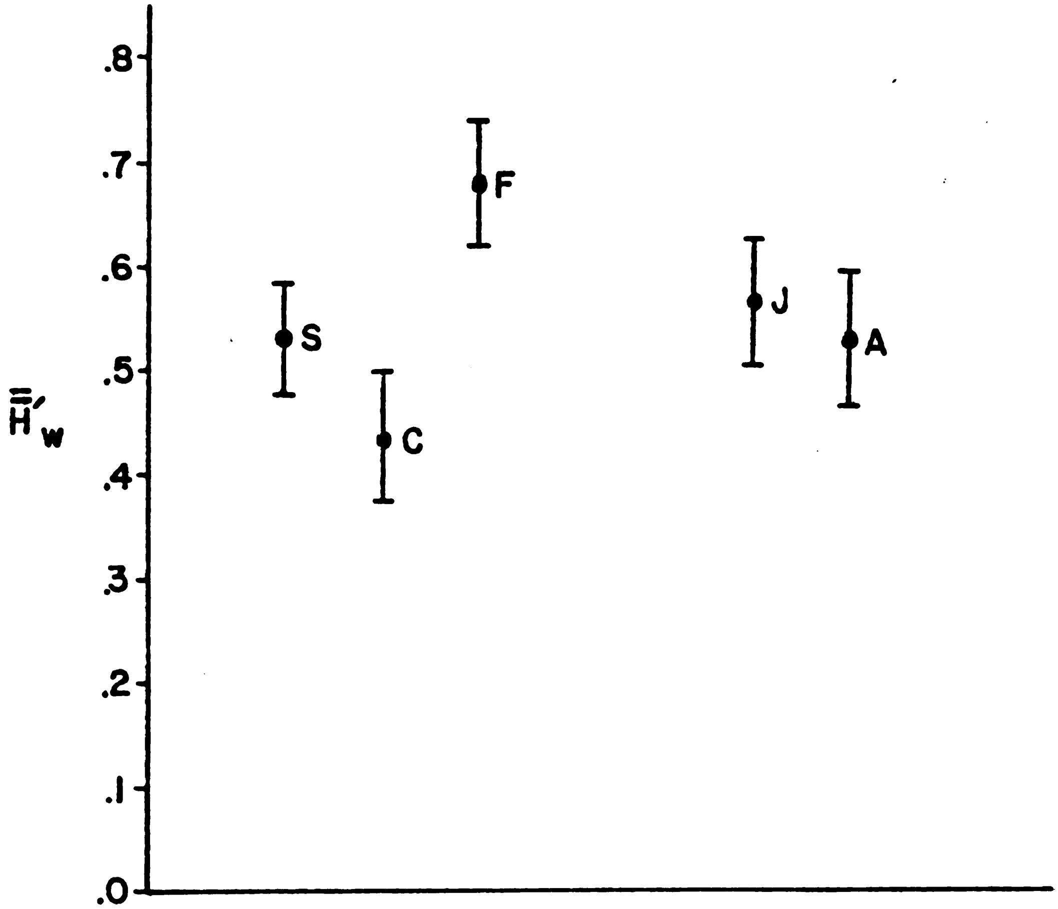

Figure 11. Mean ± 1 s.e. feeding diversity for the Stable (S), Choice (C), Fluctuating (F), Juvenile (J), and Adult (A) groups.

whereas 42% of the wild-caught mice (14 of 33) crossed; these two groups obviously differ in experience. Whether experience is actually a factor, and if so what type of experience is important, cannot be determined from the available data.

Three conclusions follow from the results of the experiment on neophobia. First, experience with diverse flavors decreases neophobia. This follows from the observation that mice with diverse experience drank significantly more sugar-water at testing than those which had been exposed only to water prior to testing. Second, the effects of experience on neophobia are temporally limited. Mice with different experience did not differ when testing was delayed for six weeks after experience. Third, in contrast to experience, age does not affect neophobia. Among animals that received only water, there was no significant difference between those tested at 44 days and those tested at 88 days.

Like neophobia, the feeding diversity of adults can be affected by early experience (Experiment 4.3). This experiment also provides information about the types of experience that influence feeding diversity.

Diversity was not "imprinted"; that is, the mice did not continue into adulthood the patterns that were established during rearing. The relationship between the Fluctuating and Stable groups reversed between rearing and testing. The daily diversity of the Fluctuating group during development had to be zero because they received one food per day. Since the Stable group was forced to eat most of the four foods daily during rearing, this group had a high diversity. However, at testing, the Fluctuating group had higher diversity than the Stable group.

Neither the opportunity to choose, nor the type of food, nor the abundance of food encountered during rearing determined later diversity. If choice were an important variable, the feeding diversity of the Fluctuating, Stable, and Adult groups, which had virtually no choice of what to eat, would be the same, and different from that of the Choice group. If the type of food were important, the Fluctuating, Stable, and Choice groups would be the same and different from the Adult group raised on lab chow. If abundance of food were important, the Stable (2.8 g) and Fluctuating (2.5 ± 1.5 g) groups would be similar and different from the Choice (11.2 g) and Adult (200+ g) groups. However, the abundance of food was not exactly the same in the Stable and Fluctuating groups ($2.5 \pm 1.5 \neq 2.8$), or in other groups, and thus must remain a possible variable.

Stability of the diet is the most reasonable variable explaining these data. Stability and its converse, fluctuation, refer to the predictability and constancy in the abundance and types of food in the diet. This is the characteristic that the Stable and Choice groups share that is different in the Fluctuating group. The Stable and Choice groups "knew" what tomorrow's diet would be; the Fluctuating group did not. Supporting this conclusion, the Adult group, reared under very different but stable conditions, showed the same average diversity as the Stable group.

Finally, age *per se*, did not influence feeding diversity in *P. leucopus*. The Juvenile group had virtually the same average feeding diversity as the Adult group, which were raised under standard, controlled laboratory conditions. Rather, it is the experience that is accrued with age that determines later feeding diversity.

In summary, although age distinguished isolated and contiguous immigrants, it was not sufficient to explain the behavioral differences observed. Young and older lab-reared P. leucopus did not differ significantly in barrier-crossing, neophobia, or feeding diversity. However, behavioral differences between groups of lab-reared mice could be produced by manipulation of early experience. Mice exposed to a number of novel-flavored fluids were less neophobic than mice which had only been exposed to water. Individuals exposed to an unpredictable diet became more generalized feeders than those exposed to stable diets.

GENERAL DISCUSSION

The general hypothesis tested in this work was that *Peromyscus leucopus* which disperse across habitat discontinuities differ qualitatively from conspecifics which disperse within continuous habitat. Demographic and behavioral attributes were studied. Briefly, the results of the experiments showed that immigrants to isolated patches of habitat were younger, more prone to cross barriers in the laboratory, and less neophobic than within-woodlot dispersants. The two groups did not differ consistently in sex ratio, in proportion of the animals of sufficient size to breed, or in reproductive condition. The two immigrant groups did not differ in feeding diversity, but together they were more generalized feeders than residents. None of the behavioral differences seen could be attributed to age, but experience affected neophobia and feeding diversity. Mice exposed to novel fluids or an unpredictable diet became less neophobic and more generalized feeders, respectively. Thus, there are data to support the initial prediction. In some respects, *P. leucopus* which have dispersed across unforested areas differ from those which have dispersed within continuous habitat.

In this section, some implications of the general strategy observed for *P. leucopus* will be discussed, and some areas for future research will be proposed. In addition, the data gathered here will be compared with information collected by other investigators, and possible reasons for discrepancies will be discussed.

Fairbairn (1977, 1978a) found significantly more male than female P. maniculatus dispersing during the breeding season. In addition, dispersing males were less reproductively active than dispersing females. In accordance with the ideas of Sadlier (1965) and Healey (1967), Fairbairn concluded that the differential responses of the sexes reflected different social pressures acting on males and females. Young males are supposedly forced to disperse by aggressive, resident males, whereas females are recruited into the population.

The work here does not suggest such a sexual dichotomy. There were slight trends among contiguous immigrants for males to outnumber females, and, similarly, some surpluses of males were seen in the isolated immigrant group relative to the contiguous immigrants. However the differences were not statistically significant. These trends can be accounted for by data from several species of Peromyscus which indicate that (1) males disperse farther than females (Allred and Beck, 1963; Blair, 1958; Blair and Kennerly, 1959; Dice and Howard, 1951; Nicholson, 1941; Smith, 1968), and (2) males have larger home ranges than females (see Stickel, 1968). Both of these facts suggest that a slight surplus of males would be expected in each of the immigrant groups, as was seen.

The major result of the investigation of sex distribution in this study was that, for every trapping period, the sex ratios of isolated and contiguous immigrants did not differ. Thus there is no evidence that one sex chooses, or is forced, to cross barriers in greater numbers than the other sex. Furthermore, resident and immigrant P. leucopus have similar sex ratios, indicating that no differential factors influence males and females to remain sedentary or disperse. Two additional sets of data from within the present study reinforce this conclusion. First, although the reproductive condition of immigrants will be discussed in detail below, it should be noted here that, for all groups, the degrees of reproductive activity of males and females are equivalent. This is true for both immigrant groups even though there is considerable variation in reproductive activity of the immigrants among the trapping periods (see Figures 6 and 7). These data suggest that dispersing males and females encounter similar environmental conditions. Second, in the studies of the development of barrier crossing, neophobia, and feeding diversity (Chapter 4), there were no differences between males and females. This indicates that males and females have similar capacities to respond, and respond similarly, to experiential factors.

The reason for the difference in results between this work and the work of Fairbairn (1977, 1978a) cannot be stated with certainty. One possibility is the use of different species. Hansen and Batzli (1978) found that supplemental food did not affect recruitment of either sex of _P. leucopus_ in spring and summer. Harland _et al._ (1978) studied _P. leucopus_ and found a difference in sex ratio between residents and immigrants only within a subadult age class; no differences were found among either adults or juveniles. A difference only within a narrow age class strongly suggests to me that differential dispersal of the sexes is not a prominent feature in the dispersal of _P. leucopus_. On the other hand, a number of the isolated immigrants in this study would presumably be considered subadults by Harland _et al._ (based on pelage), and thus a significant surplus of males might be expected among the isolated immigrants. However, a precise comparison of the two studies is difficult because of the different age classes used. Nonetheless, the evidence from this study indicates that barriers do not differentially affect males and females.

Age, as indexed by the weight of the eye lens, was the only demographic variable that distinguished isolated and contiguous immigrants. According to this method, the average age of contiguous immigrants was the same as that of the residents. This fact, in in conjunction with the similar proportions of adults and juveniles in the two groups indicates that, in continuous habitat, *P. leucopus* of any age are equally likely to invade a vacant area. That is, contiguous immigrants are a cross-section of the resident population in terms of age. In contrast to this, isolated immigrants had a lower average age than contiguous immigrants and residents. This difference was restricted to animals of adult size; juveniles of the two groups were the same. Thus *P. leucopus* which disperse across barriers are not a cross-section of the resident population; they are predominantly young adults.

Old adult *P. leucopus* will move within contiguous habitat. Prior to dispersal some of these individuals would probably qualify as residents with relatively stable home ranges, yet in the presence of vacant habitat they will disperse into it (see Stickel, 1946). However, young adults, presumably making their first major dispersal, will cross habitat discontinuities. The precise reason for the different responses of the two age groups to barriers is unknown. The results of the behavioral experiments show that the age differences observed among the groups are not due strictly to some property of age. Age had no effect on barrier crossing, neophobia, or feeding diversity -- variables in which differences were found among wild-caught members of the treatment groups.

Only two ages were tested in the laboratory, but the ages chosen for the studies of barrier crossing and neophobia are reasonable approximations of the mean ages of the treatment groups from the demographic study. Clark (1938) found the mean age at first estrus to be 46.2 days (see also Rogers and Beauchamp, 1974), and the "young" age for the laboratory studies was about 50 days (Experiments 4.1 and 4.2). Since isolated immigrants were predominantly juveniles and recently-matured adults, they were probably at about this age when they dispersed. The "old" age used in the laboratory studies was about 90 days. By this time a mouse has spent approximately half of its life as an adult, and this probably resembles the condition for older residents and contiguous immigrants. In addition, in the study of the development of feeding diversity (Experiment 4.3), mice were tested as weanlings and older adults. This large age difference would tend to maximize the chances of observing an age effect, if one exists. Thus it would appear that an ontogenetic effect of age, _per se_, does not account for the age differential between isolated and contiguous immigrants.

There is, however, an alternative method by which age could indirectly affect the timing of dispersal. The studies on the development of neophobia and feeding diversity showed that experience influenced these behaviors (Experiments 4.2 and 4.3). In both of these studies, the experience was administered beginning at weaning. It is possible that older mice are less responsive to such environmental factors. Capretta *et al.* (1975) found that experience with diverse tastes decreased neophobia in immature rats, but not in rats that were older at the start of training. The effects of the timing of experience on feeding diversity and neophobia were not tested here. However, preliminary data suggest *P. leucopus* exposed to the five novel flavors from 65-84 days of age do not differ in neophobia at 88 days from mice that received only water during rearing (Tardif, unpublish.). If a sensitivity to these experiences is a prerequisite for dispersal across a barrier, then young mice would cross barriers while older individuals would not. Lidicker (1962, 1975) suggested that "pre-saturation" dispersal occurs prior to the population reaching the carrying capacity of the environment. This hypothesis requires that animals be sensitive to environmental changes before conditions become critical. If age accounts for sensitivity to such conditions, then such dispersal might occur within a limited segment of the population.

Precise comparisons between this and other studies in regard to the age of immigrants are difficult because of the variety of techniques used. The adult condition has been established according to (1) commencement of reproductive activity (e.g. Howard, 1949), (2) body weight (e.g. Fairbairn, 1978a), and (3) pelage (e.g. Harland *et al.*, 1978). However, criteria which divide animals into two or three age classes cannot distinguish age differences within the classes, and all systems of classification are of dubious quality near the boundaries between classes. The present study shows that classification of mice as adults and juveniles on the basis of body size was insufficient to detect the effect of barriers on the age of immigrants. The additional variable of eye lens weight, a precise, continuous measurement, did reveal a difference. Unfortunately, no other studies of dispersal have employed this technique.

Dispersal of Peromyscus often occurs at about the age of puberty (Fairbairn, 1977, 1978a; Hansen and Batzli, 1978; Harland *et al.*, 1978; Petticrew and Sadlier, 1974; Smith, 1968; for reviews see Stickel, 1968 and Terman, 1968). These animals are presumably leaving the parental home range. This study has shown that this is the age of most isolated immigrants. Older adult Peromyscus are also known to disperse (e.g. Gentry, 1966; Harland *et al.*, 1978; for reviews see Stickel, 1968 and Terman, 1968). A major finding of this study is that, in continuous habitat, older individuals move into vacant areas proportionately as frequently as members of the age classes usually thought of as dispersers. These older individuals, however, move less frequently between woodlots. In contrast to previous studies, age as a variable in dispersal was significant in respect to different types of dispersal (within and between woodlots) and perhaps as discussed above, in respect to the interaction of age and experience.

The reproductive activity of isolated and contiguous immigrants is important, but the variability between trapping periods makes broad conclusions precarious. The results of this study differ to some degree with most of the existing literature. However, as with age, differences in technique make exact comparisons difficult. For example, in the most extensive recent study of dispersal in Peromyscus, Fairbairn (1977, 1978a) classified female *P. maniculatus* as reproductively mature on the basis of nipple size and vaginal perforation. This technique is mandated by the use of live animals that must remain in the population, but does not provide the accuracy available from autopsy. Perforate females may not actually be breeding, may be in the early (undetectable) stages of pregnancy, or may be between litters; these conditions cannot be distinguished on live animals. Note that the small litter size and early stages of pregnancy, particularly among isolated immigrants, resulted in them not being "obviously pregnant". Harland *et al.* (1978) used both a live-trap and a snap-trap grid to study the dispersal of *P. leucopus*, but made only fleeting reference to the results of autopsies. Thus this is the first large-scale study in which detailed reproductive information is available for dispersing *Peromyscus*.

June 1976 was the only trapping period in which the two immigrant groups were significantly different; isolated immigrants were highly reproductive while contiguous immigrants were reproductively inactive. In June 1977 both groups were as reproductively active as residents (see Figures 6 and 7). The reason for the different responses of the contiguous immigrants is unknown. However, the density of the residents was approximately nine times higher in June 1976 than in June 1977. This invites speculation that the reproductive condition of contiguous immigrants varies with population density. This hypothesis was tested from within the data. A linear regression of mean testes weight for contiguous immigrants versus density of residents for the contiguous plots in June 1976 and 1977 ($n = 6$) has a slope of -0.665 ($r = -0.78$ for H_0: $r = 0$, $.10 > P > .05$). This suggests that as resident density increases, there is a trend for reproductive activity of contiguous immigrants to decrease. The number of data points are few, and I suspect that significant results would be found if more data were available.

Still, no satisfactory explanation can be given for the difference between the two Junes. King (1973) has pointed out that density in itself is not a causative mechanism; rather, changes in density affect environmental conditions. It is possible that some animals were inhibited from reproducing when density was high. Laboratory populations of rodents show curtailment of reproductive maturation in young at high densities (e.g. Terman, 1965), but the data collected do not provide information on whether such forces were acting here. Alternatively, the lack of a large surplus in the population in June 1977 may have resulted in the contiguous immigrants being mostly older, resident animals from peripheral areas.

If social factors within resident populations of June 1976 reduced reproduction, it is possible that individuals moving to isolated woodlots became reproductively active after leaving the dense populations. It seems unlikely that the mice commenced reproducing after dispersal because of the short duration of dispersal and the stage of pregnancy of gravid immigrants. The best data available (Howard, 1949) suggest that the dispersal movements of mice take only one or two nights. It is also unlikely, with continuous trapping, that the mice resided in the isolated woodlots long before capture. The mean crown-rump length of embryos from isolated immigrants was 6.00 mm. In Mus musculus this length occurs at approximately 11 days of gestation (Rugh, 1968). While only a crude estimate, this shows that isolated immigrants had been impregnated a considerable time prior to capture.

With the exception of the contiguous immigrants in June 1976, immigrant reproductive activity was high in June and low in September.

Low reproductivity among immigrants is the typical condition reported for *Peromyscus*. All of the *P. maniculatus* studied by Howard (1949) dispersed prior to achieving sexual maturity. Fairbairn (1978a) found that dispersing male *P. maniculatus* were less reproductively active than residents. Similar data have been reported by other investigators (e.g. Burt, 1940; Nicholson, 1941). Such low levels of reproductive activity are certainly evident in both Septembers for both immigrant groups (even though contiguous immigrants are older than isolated immigrants). In sharp contrast to this, immigrants tend to be as reproductively active as residents in June. The reason for this is unknown. Fairbairn (1978a) claims that non-reproductive males are forced to disperse by aggressive resident males during the breeding season (see also Healey, 1967; Sadlier, 1965). This view is not, however, consistent with the data collected here. In the present study, all trapping was done during the breeding season as evidenced by the high and constant reproductive levels of residents (see Figures 6 and 7). Thus aggression during the breeding season could not account for the differences between June and September. In addition, males and females showed equivalent reproductive activity in each trapping period, indicating that, even if social pressures are important, the sexes face similar conditions. Similarly, aggression by breeding females (Enders, 1977; Hansen and Batzli, 1978) cannot account for the difference.

An alternative cause of the difference in reproductive activity between June and September is a delay in maturation of animals born later in the breeding season. Burt (1940) and Rintamaa *et al.* (1976) have noted that *Peromyscus* born in the autumn do not reproduce until the following spring (see also Howard, 1949). Still, mice dispersing as young adults in mid-September are probably born sometime in July, and it is unknown if the autumnal delay occurs this early in the year. This problem could be resolved by allowing immigrants to remain on the grids after dispersal in September. If they commenced reproducing after dispersal, then some form of social factor is to be suspected; if they remained non-reproductive until the following spring, then the autumnal deferment of reproduction may be responsible. It is possible that some individuals of both types might be found (some reproduction was seen among September immigrants). That is, some mice might begin reproducing after dispersal in September, while others wait until spring. If this is so, it would be interesting to compare the reproductive success of the two groups.

Regardless of the mechanisms that produced these patterns, the presence of highly reproductive immigrants is interesting and has rather significant consequences. Reports of dispersal by pregnant female rodents are few and not usually systematic. Some *Microtus oeconomus* make seasonal movements between habitats while pregnant (Tast, 1966). Myers and Krebs (1971) noted the movement of pregnant *Microtus pennsylvanicus* and *M. ochrogaster* into trapped-out areas (see also Van Vleck, 1968). Jannett (1978) found that some *Microtus montanus* abandon their nest and young at about fifteen days postpartum, move, and establish a new nest while pregnant. Some *Mus musculus* may also disperse while pregnant (Rowe *et al.*, 1953; Strecker, 1954). Stoddart (1970) noted the dispersal of an *Arvicola terrestris* that was probably pregnant. Harland *et al.* (1978) make only a fleeting reference to the occurrence of pregnant *P. leucopus* on a removal grid.

In this study, the majority of adult female isolated immigrants dispersing in June were pregnant. This strategy may allow for the rapid exploitation of small patches of habitat. The necessity of finding a mate is obviated. A population founded by a single, pregnant female would be closely related and could saturate a small patch of habitat very quickly. This sequence of events, of course, would depend on how closed such a population is to further immigration and whether the young remained to reproduce or dispersed.

The paternity of the litter of dispersing females is intriguing but inaccessible by current techniques. Females are impregnated prior to dispersal. Mating with a relative would result in a founding population with relatively little genetic variation. Howard (1949) estimated that 4-10% of the litters he observed were produced by either parent-offspring or sibling matings. Rasmussen (1964) hypothesized that the lack of heterozygotes he observed in _P. maniculatus_ was due to inbreeding. Skryja (1978) found that father-daughter matings in _P. eremicus_ reproduced as well as unrelated pairs. Finally, it is interesting to note the benefit accrued to a male which remains in his home area, but impregnates an incipient disperser. His genes are "dispersed" at little or no risk to himself.

Upon first consideration, dispersal while pregnant seems to be adding an additional burden to an already risky undertaking. Two facts suggest that this might not be the case. First, female _Peromyscus_ do not show increased energy demands during pregnancy, although energy consumption increases drastically for lactation (Millar, 1975; Sadlier _et al._, 1973; Stebbins, 1977). Thus there appears to be no additional energy demands associated with this strategy. Second, immigrants had small litters, and isolated immigrants tended to be in the early stages of pregnancy. Such data argue against reduced mobility or excessive nutritional demands hindering this strategy. However, it is necessary for females to be able to meet the demands of lactation. The generalized feeding behavior and reduced neophobia observed in the laboratory would be of help in such an endeavor. Increased hoarding might also be expected.

Only two previous studies have systematically investigated behavioral differences between residents and immigrants. Myers and Krebs (1971) examined exploratory behavior, general activity, and aggressiveness in *Microtus pennsylvanicus* and *M. ochrogaster*. Fairbairn (1978b) similarly tested resident and immigrant *P. maniculatus*. These studies, particularly the tests of aggression, were primarily concerned with factors that might prompt dispersal. In the present study, a different approach has been taken. Neophobia and feeding diversity were chosen as possible behavioral correlates of dispersal that might be advantageous to a dispersant in exploiting a new environment. Isolated immigrants were less neophobic and tended to be more generalized feeders than residents and contiguous immigrants. Thus animals which have dispersed across a barrier are behaviorally "equipped" to deal with the new and diversified foods in their new surroundings.

Isolated immigrants were also more prone to cross barriers under laboratory conditions, which further reinforces the validity of the distinction between within-woodlot and between-woodlot dispersants. It is interesting to note that isolated immigrants crossed the laboratory barriers in the absence of social pressures and in the presence of abundant food, water, and shelter. This may represent some genetic predisposition to disperse, as has been proposed by Fairbairn (1978b) and Howard (1960). It is also possible that this adventurous behavior pattern was developed as a result of experience. The importance of experience in neophobia and feeding diversity makes me inclined to suspect experiential factors. This hypothesis could be readily tested by exposing mice to various types of experience (resource deprivation, aggression, etc.) and then testing them in the barrier apparatus.

All behaviors are the product of both genetics and experience; the relative contribution of each may vary. The role of genetics was not systematically investigated for any of the behaviors studied here. Nonetheless it appears that genetics does not play a major role in the behavioral differences observed here. There are two reasons to suspect this. First, there were no obvious differences between the offspring of various parents in any of the developmental tests. The parents were usually pairs of wild-caught residents, contiguous immigrants, and isolated immigrants. Second, conditions imposed in the developmental tests on neophobia and feeding diversity were sufficient to make lab-reared mice almost as generalized as wild-caught individuals. Studies of the heritability of the three behaviors should be done. They will provide more detailed information on the role of genetics in these correlates of dispersal and, possibly, on dispersal itself. For the moment, however, it seems wise to conclude that experiences, perhaps obtained at certain ages, are the major factors causing the differences observed. Thus the strategy of dispersing P. leucopus appears to involve a considerable amount of behavioral plasticity. This plasticity allows individuals to respond quickly to environmental changes such as those encountered by dispersants. It also may help account for the variety of individuals found to disperse in the demographic study.

P. leucopus which have dispersed between woodlots were behaviorally more generalized than either those dispersing within woodlots or resident mice. A major question emerging from this observation is whether (1) animals possessing a particular constellation of behaviors are more apt to disperse between woodlots, or (2) mice develop these characteristics as a result of dispersing. In other words, do generalists disperse across barriers or do dispersants across barriers become generalists? In order to test this directly, the behavior of an individual must be known both before and after dispersal in the field -- not an easy task. It is possible that the entire dispersal sequence in an adequate number of P. leucopus could be obtained in an area where there were only two woodlots. It is also necessary to have a behavioral test that does not excessively disrupt the population. I believe the sucrose-and-water test of neophobia used in the laboratory here could provide such a tool. Mice could be live-trapped in both woodlots and housed in cages in the woodlots during the daytime with food and shelter but no water. Drinking tubes with water and sucrose could then be presented at sundown. The absence of water in the trap and during the following day would insure sufficient thirst for the test. Mice could then be marked and released near the beginning of their normal time of activity. Mice dispersing between woodlots could theoretically be tested sometime immediately before dispersing and sometime after dispersal. Even if most mice were lost after initial testing, the neophobia of disappearing versus remaining mice could be obtained. In this case mortality would be a confounding variable.

Similarly, the duration of these behaviors after their development is uncertain. It is possible that once mice have become generalized feeders or less neophobic they remain so. Alternatively, these types of behavior may only occur while an individual is becoming established. Once an area is familiar to an animal, the individual may become more specialized in its behavior. This latter alternative seems the most likely because in the study of the development of neophobia, the groups with limited and diverse experience did not differ when testing was delayed for six weeks after the experience (unlike the rats of Capretta _et al._, 1975). Also, wild-caught residents, which probably include mice that had dispersed at some time, showed the most specialized behavior. More extensive testing done on the maintenance or decay of neophobia and feeding diversity following establishment of generalized behavior should clarify this issue.

In summary, _Peromyscus leucopus_ which have dispersed between woodlots possess a constellation of characters that distinguishes them from residents and mice that have dispersed within continuous habitat. Behaviorally, barrier-crossers were more likely to cross laboratory barriers, were less neophobic, and tended to be more generalized feeders. Isolated immigrants also were younger, as evidenced by eye lens weight, than either residents or contiguous immigrants, but age itself was not sufficient to account for the observed behavioral differences. Rather, _P. leucopus_ changed their behavior in response to experience of various types. This behavioral plasticity would benefit an individual attempting to become established in a new area. It is unknown whether the experience and consequent behaviors facilitate the initiation of dispersal or are developed as a result of dispersal. Sex and the proportions of adults and juveniles distinguished neither the two immigrant groups, nor residents and immigrants. Males and females were equally represented in all groups and all groups were predominantly adults. Isolated immigrants were highly reproductive in June and reproductively inactive in September. Most adult female isolated immigrants were pregnant in June. Contiguous immigrants showed variable reproductive activity in June and were non-reproductive in September. Although reproductive activity does not distinguish the two immigrant groups, the dispersal of pregnant females to isolated patches of habitat could result in rapid exploitation of available areas.

BIBLIOGRAPHY

BIBLIOGRAPHY

Alcock, J. 1975. Animal Behavior: an Evolutionary Approach. Sinauer Assoc., Inc., Sunderland, Massachusetts, xi + 547 pp.

Allred, D. and D.E. Beck. 1963. Range of movement and dispersal of some rodents at the Nevada atomic test site. J. Mamm., 44:190-200.

Ambrose, H.W. III. 1972. Effect of habitat familiarity and toe-clipping on rate of owl predation in Microtus pennsylvanicus. J. Mamm., 53:909-912.

Anderson, P.K. 1961. Density, social structure, and nonsocial environment in house-mouse populations and the implications for regulation of numbers. Transact. New York Acad. Sci., Ser. II, 23:447-451.

Anderson, P.K. 1970. Ecological structure and gene flow in small mammals. Symp. Zool. Soc. Lond., 26:299-325.

Andrzejewski, R. and H. Wroclawek. 1961. Mortality of small rodents in traps as an indication of the diminished resistance of the migrating part of a population. Bull. Acad. Polonaise Sci., Cl. 2, 9(12):491-492.

Andrzejewski, R. and H. Wroclawek. 1962. Settling by small rodents a terrain in which catching out had been performed. Acta Theriol., 6:257-274.

Armitage, K.B. 1962. Social behavior of a colony of the yellow-bellied marmot (Marmota flaviventris). Anim. Behav., 10:319-331.

Armitage, K.B. 1977. Social variety in the yellow-bellied marmot: a population-behavioral system. Anim. Behav., 25:585-593.

Balaban, M. 1975. Behavioral ontogeny. pp. 43-59 in The Behavior of Domestic Animals (E.S.E. Hafez, ed.). Baillere Tindall, London, xii + 532 pp.

Barnett, S.A. 1958. An analysis of social behavior in wild rats. Proc. Zool. Soc. Lond., 130:107-152.

Bateson, P.G.P. 1976. Specificity and the origins of behavior. Advances in the Study of Behavior, 6:1-20.

Batzli, G.O., L.L. Getz, and S.S. Hurley. 1977. Suppression of growth and reproduction of microtine rodents by social factors. J. Mamm., 58:583-591.

Beckwirth, S.L. 1954. Ecological succession on abandoned farm lands and its relationship to wildlife management. Ecol. Monogr., 24:349-376.

Beer, J.R., P. Lukens, and D. Olson. 1954. Small mammal populations on the islands of Basswood Lake, Minnesota. Ecology, 35:437-445.

Bekoff, M. 1977. Mammalian dispersal and the ontogeny of individual behavioral phenotypes. Amer. Nat., 111:715-732.

Bendell, J.F. 1959. Food as a control of a population of white-footed mice, Peromyscus leucopus noveboracensis (Fischer). Canad. J. Zool., 37:173-209.

Bishop, O.N. 1966. Statistics for Biology. Houghton Mifflin Co., New York, x + 182 pp.

Blair, W.F. 1958. Effects of x-irradiation on a natural population of the deermouse. Ecology, 39:113-118.

Blair, W.F. and T.E. Kennerly Jr. 1959. Effects of x-irradiation on a natural population of the wood-mouse (Peromyscus leucopus). Texas J. Sci., 11:137-149.

Boonstra, R. 1978. Effect of adult townsend voles (Microtus townsendii) on survival of young. Ecology, 59:242-248.

Braveman, N.S. and P.S. Jarvis. 1978. Independence of neophobia and taste aversion learning. Anim. Learn. Behav., 6:406-412.

Briese, L.A. and M.H. Smith. 1974. Seasonal abundance and movement of nine species of small mammals. J. Mamm., 55:615-629.

Bronson, F.H. 1964. Agonistic behavior in woodchucks. Anim. Behav., 12:470-478.

Brown, J.L. 1975. The Evolution of Behavior. W.W. Norton and Co., New York, xix + 761 pp.

Brown, R.Z. 1953. Social behavior, reproduction, and population change in the house mouse (Mus musculus). Ecol. Monogr., 23:217-240.

Burt, W.H. 1940. Territorial behavior and populations of some small mammals in southern Michigan. Misc. Pub. Mus. Zool. Univ. Mich., 45:1-58.

Burt, W.H. 1957. Mammals of the Great Lakes Region. Univ. Mich. Press, Ann Arbor, xv + 246 pp.

Burt, W.H. and R.P. Grossenheider. 1976. A Field Guide to the Mammals. Houghton, Mifflin Co., Boston, Third edition, xxv + 289 pp.

Calhoun, J.B. 1948. Mortality and movements of brown rats (Rattus norvegicus) in artificially supersaturated populations. J. Wildlf. Mgmt., 12:167-172.

Calhoun, J.B. 1963. The social use of space. pp. 1-187 in Physiological Mammalogy, vol. 1 (W. Mayer and R. VanGelder, eds.). Academic Press, New York, xii + 381 pp.

Calhoun, J.B. and W.L. Webb. 1953. Induced emigrations among small mammals. Science, 117:358-360.

Cameron, G.N. 1977. Experimental species removal: demographic responses by Sigmodon hispidus and Reithrodontomys fulvescens. J. Mamm., 58:488-506.

Capretta, P.J., J.T. Petersik, and D.J. Stewart. 1975. Acceptance of novel flavors is increased after early experience of diverse tastes. Nature, 254:689-691.

Carl, E.A. 1971. Population control in arctic ground squirrels. Ecology, 52:395-413.

Christian, J.J. 1970. Social subordination, population density, and mammalian evolution. Science, 168:84-90.

Christian, J.J. 1971. Fighting, maturity, and population density in Microtus pennsylvanicus. J. Mamm., 52:556-567.

Christian, J.J. and C.D. LeMunyan. 1958. Adverse effects of crowding on lactation and reproduction of mice and two generations of progeny. Endocrinol., 63:517-529.

Christianson, L. 1977. Winter movements of Peromyscus across a lake in northern Minnesota. J. Mamm., 58:244.

Clark, F.H. 1938. Age of sexual maturity in mice of the genus Peromyscus. J. Mamm., 19:230-234.

Corthum, K.W., Jr. 1967. Reproduction and duration of placental scars in the prairie vole and the eastern vole. J. Mamm., 48:287-292.

Cowley, J.J. and D.R. Wise. 1972. Some effects of mouse urine on neonatal growth and reproduction. Anim. Behav., 20:499-506.

Crowcroft, P. and F.P. Rowe. 1958. The growth of confined colonies of the wild house mouse: the effect of dispersal on female fecundity. Proc. Zool. Soc. Lond., 131:357-365.

Dalmat, H.T. 1942. A new parasitic fly (Cuterebridae) from the northern white footed mouse. J. New York Ent. Soc., 50:45-59.

Davis, D.E. and J.T. Emlen. 1948. The placental scar as a measure of fertility in rats. J. Wildlf. Mgmt., 12:162-166.

Davis, D.E. and J.J. Christian. 1956. Changes in Norway rat populations induced by introduction of rats. J. Wildlf. Mgmt., 20:378-383.

Davis, D.E., J.J. Christian, and F. Bronson. 1964. Effect of exploitation on birth, mortality, and movement rates in a woodchuck population. J. Wildlf. Mgmt., 28:1-9.

DeLong, K.T. 1967. Population ecology of feral house mice. Ecology, 48:611-634.

Dice, L.R. and W.E. Howard. 1951. Distance of dispersal by prairie deer mice from birthplace to breeding sites. Contrib. Lab. Vert. Biol. Univ. Mich., 50:1-15.

Domjan, M. 1977. Attenuation and enhancement of neophobia for edible substances. pp. 151-179 _in_ Learning Mechanisms in Food Selection (L.M. Barker, M.R. Best, and M. Domjan, eds.). Baylor Univ. Press, xiv + 632 pp.

Dunford, C. 1977. Social system of round-tailed ground squirrels. Anim. Behav., 25:885-906.

Emlen, J.T., A.W. Stokes, and C.P. Windsor. 1948. The rate of recovery of decimated populations of brown rats in nature. Ecology, 29:133-145.

Enders, J.E. 1977. Social interactions between confined juvenile and adult _Peromyscus maniculatus bairdi_: effects of social factors on juvenile settlement and growth. Unpublish. Ph.D. dissertation, Michigan State Univ., East Lansing, 180 pp.

Errington, P.L. 1963. Muskrat Populations. Iowa State Univ. Press, Ames, 665 pp.

Fairbairn, D.J. 1977. The spring decline in deermice: death or dispersal. Canad. J. Zool., 55:84-92.

Fairbairn, D.J. 1978a. Dispersal of deer mice, _Peromyscus maniculatus_. Oecologia, 32:171-193.

Fairbairn, D.J. 1978b. Behaviour of dispersing deer mice (_Peromyscus maniculatus_). Behav. Ecol. and Sociobiol., 3:265-282.

Fitch, H.S. 1948. Habits and economic relationships of the tulare kangaroo rat. J. Mamm., 29:5-35.

Flowerdew, J.R. 1974. Field and laboratory experiments on the social behavior and population dynamics of the wood mouse (Apodemus sylvaticus). J. Anim. Ecol., 43:499-511.

Freeland, J.W. 1974. Vole cycles: another hypothesis. Amer. Nat., 108:238-245.

Garten, C.T. and M.H. Smith. 1974. Movement by oldfield mice and population regulation. Acta Theriol., 19:513-514.

Gentry, J.B. 1966. Invasion of a one-year abandoned field by Peromyscus polionotus and Mus musculus. J. Mamm., 47:431-439.

Getz, L.L. and M.L. Prather. 1975. A method to prevent removal of trap bait by insects. J. Mamm., 56:955.

Gibson, E.J. 1969. Principles of Perceptual Learning and Development. Appleton-Century-Crofts, New York.

Gill. J.L. 1978. Design and Analysis of Experiments, vol. 1. The Iowa State Univ. Press, Ames, xiii + 409 pp.

Gray, L. 1977. The feeding diversity of deer mice. Unpublish. Ph.D. dissertation, Michigan State Univ., East Lansing, 84 pp.

Gray, L. and R.R. Tardif. in press. The development of feeding diversity in deermice. J. Comp. Physiol. Psych.

Hall, R.W. and K.R. Kelson. 1959. The Mammals of North America. The Ronald Press Co., New York, 1162 pp.

Halpin, Z.T. and T.P. Sullivan. 1978. Social interactions in island and mainland populations of the deer mouse, Peromyscus maniculatus. J. Mamm., 59:395-401.

Hansen, L. and G.O. Batzli. 1978. The influence of food availability on the white-footed mouse: populations in isolated woodlots. Canad. J. Zool., 56:2530-2541.

Harland, R.M., P.J. Blancher, and J.S. Millar. 1978. Demography of a population of Peromyscus leucopus. Canad. J. Zool., 57:323-328.

Healey, M.C. 1967. Aggression and self-regulation of population size in deer mice. Ecology, 48:377-392.

Helmreich, R.L. 1960. Regulation of reproductive rate by intra-uterine mortality in the deer mouse. Science, 132:417-418.

Howard, W.E. 1949. Dispersal, amount of inbreeding and longevity in a local population of prairie deer mice on the George Reserve, southern Michigan. Contrib. Lab. Vert. Biol. Univ. Mich., 43:1-50.

Howard, W.E. 1960. Innate and environmental dispersal of individual vertebrates. Amer. Midland Nat., 63:152-161.

Howard, W.E. 1965. Interaction of behavior, ecology, and genetics of introduced animals. pp. 461-484 in The Genetics of Colonizing Species (H.G. Baker and G.L. Stebbins, eds.). Academic Press, New York.

Jackson, W.B. 1952. Populations of the woodmouse (Peromyscus leucopus) subjected to the applications of DDT and parathion. Ecol. Monogr., 22:259-281.

Jameson, E.W., Jr. 1950. Determining fecundity in male small mammals. J. Mamm., 31:433-436.

Jannett, F.J., Jr. 1978. The density-dependent formation of extended maternal families of the montane vole Microtus montanus nanus. Behav. Ecol. and Sociobiol., 3:245-263.

Joule, J. and G.N. Cameron. 1975. Species removal studies. I. Dispersal strategies of sympatric Sigmodon hispidus and Reithrodontomys fulvescens populations. J. Mamm., 56:378-396.

Kemp, G.A. and L.B. Kieth. 1970. Dynamics and regulation of red squirrel (Tamiasciurus hudsonicus) populations. Ecology, 51: 763-779.

King, J.A. 1955. Social behavior, social organization, and population dynamics in a black-tailed prairie dog town in the Black Hills of South Dakota. Contrib. Lab. Vert. Biol. Univ. Mich., 67:1-123.

King, J.A. 1973. The ecology of aggressive behavior. Ann. Rev. Ecol. Syst., 4:117-138.

King, J.A. 1977. Behavioral comparisons and evolution. pp. 23-36 in Genetics, Environment and Intelligence (A. Oliverio, ed.). Elsevier/North Holland Biomedical Press.

Klopfer, P.H. 1973. Behavioral Aspects of Ecology. Prentice Hall, Englewood Cliffs, New Jersey, 200 pp.

Klopfer, P.H. and R.H. MacArthur. 1960. Niche size and faunal diversity. Amer. Nat., 94:293-300.

Krebs, C.J., B.L. Keller, and R.H. Tamarin. 1969. Microtus population biology: demographic changes in fluctuating populations of M. ochrogaster and M. pennsylvanicus in southern Indiana. Ecology, 50:587-607.

Krebs, C.J., I. Wingate, J. LeDuc, J.A. Redfield, M. Taitt, and R. Hilborn. 1976. Microtus population biology: dispersal in fluctuating populations of M. townsendii. Canad. J. Zool., 54:79-95.

Lehrman, D.S. 1970. Semantic and conceptual issues in the nature-nuture problem. pp. 17-52 *in* Development and Evolution of Behavior (L.A. Aronson, E. Tobach, D.S. Lehrman, and J.S. Rosenblatt, eds.). Freeman, San Francisco, 656 pp.

Lehrman, D.S. and J.S. Rosenblatt. 1971. The study of behavior development *in* The Ontogeny of Vertebrate Behavior (H. Moltz, ed.). Academic Press, New York.

Lidicker, W.Z., Jr. 1962. Emigration as a possible mechanism permitting the regulation of population density below carrying capacity. Amer. Nat., 96:29-33.

Lidicker. W.Z., Jr. 1965. Comparative study of density regulation in confined populations of four species of rodents. Res. in Pop. Ecol., 7:57-72.

Lidicker, W.Z., Jr. 1966. Ecological observations on a feral house mouse population declining to extinction. Ecol. Monogr., 36:27-50.

Lidicker, W.Z., Jr. 1975. The role of demography in the dispersal of small mammals. pp. 73-128 *in* Small Mammals: Their Productivity and Population Dynamics (F.B. Golley, K. Petrusewicz, and L. Ryszkowski, eds.). Cambridge Univ. Press, New York, xxv + 451 pp.

Lidicker, W.Z., Jr. 1976. Social behaviour and density regulation in house mice living in large enclosures. J. Anim. Ecol., 45:677-697.

Lidicker, W.Z., Jr. and P.K. Anderson. 1962. Colonization of an island by *Microtus californicus*, analyzed on the basis of runway transects. J. Anim. Ecol., 31:503-517.

Lloyd, J.A. and J.J. Christian. 1969. Reproductive activity of individual females in three experimental freely growing populations of house mice (*Mus musculus*). J. Mamm., 50:49-59.

Louch, C.D. 1956. Adrenalcortical activity in relation to the density and dynamics of three confined populations of *Microtus pennsylvanicus*. Ecology, 37:701-713.

MacArthur, R.H. 1972. Geographical Ecology: Patterns in the Distribution of Species. Harper and Rowe, New York, 269 pp.

MarArthur, R.H. and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. Amer. Nat., 101:377-385.

Mayr, E. 1970. Populations, Species, and Evolution. The Belknap Press of Harvard Univ. Press, Cambridge, Massachusetts, xv + 453 pp.

Mazurkiewicz, M. 1972. Density and weight structure of populations of the bank vole in open and enclosed areas. Acta Theriol., 17: 455-465.

Mazurkiewicz, M. and E. Rajska. 1975. Dispersion of young bank voles from their place of birth. Acta Theriol., 20:71-81.

McCarley, H. 1959. A study of the dynamics of a population of *Peromyscus gossypinus* and *P. nuttali* subjected to the effects of x-irradiation. Amer. Midland Nat., 61:447-469.

McCarley, H. 1966. Annual cycle, population dynamics and adaptive behavior of *Citellus tridecemlineatus*. J. Mamm., 53:657-676.

M'Closkey, R.T. 1972. Temporal changes in populations and species diversity in a Califronia rodent community. J. Mamm., 53:657-676.

Metzgar, L.H. 1967. An experimental comparison of screech owl predation on resident and transient white-footed mice (*Peromyscus leucopus*). J. Mamm., 48:387-391.

Michener, G.R. and D.R. Michener. 1973. Spatial distribution of yearlings in a population of Richardson's ground squirrels. Ecology, 54:1138-1142.

Michener, G.R. and D.R. Michener. 1977. Population structure and dispersal in Richardson's ground squirrel. Ecology, 58:359-368.

Millar, J.S. 1975. Tactics of energy partitioning in breeding *Peromyscus*. Canad. J. Zool., 53:967-976.

Millar, J.S. and S.L. Iverson. 1976. Weight of the eye lens as an indicator of age in *Peromyscus*. Canad. Field Nat., 90:37-41.

Morse, D.H. 1971. The insectivorous bird as an adaptive strategy. Ann. Rev. Ecol. Syst., 2:177-200.

Myers, J.H. 1974. Genetic and social structure of feral house mouse populations on grizzly island, California. Ecology, 55:747-759.

Myers, J.H. and C.J. Krebs. 1971. Genetic, behavioral, and reproductive attributes of dispersing field voles *Microtus pennsylvanicus* and *Microtus ochrogaster*. Ecol. Monogr., 41:53-78.

Newsome, A.E. 1969. A population study of house mice temporarily inhabiting a south Australian wheatfield. J. Anim. Ecol., 38:341-359

Nicholson, A.J. 1941. The homes and social habits of the wood mouse (*Peromyscus leucopus noveboracensis*) in southern Michigan. Amer. Midland Nat., 25:196-223.

Oster, G. and B. Heinrich. 1976. Why do bumblebees major? A mathematical model. Ecol. Monogr., 46:129-133.

Oxley, D.J., M.B. Fenton, and G.R. Carmody. 1974. The effects of roads on populations of small mammals. J. Appl. Ecol., 11:51-59.

Petticrew, B.G. and R.M.F.S. Sadlier. 1974. The ecology of the deer mouse *Peromyscus maniculatus* in a coastal coniferous forest. 1. Population dynamics. Canad. J. Zool., 52:107-118.

Pielou, E.C. 1975. Ecological Diversity. John Wiley and Sons, New York, viii + 165 pp.

Pucek, Z. and J. Olszewski. 1971. Results of extended removal catches of rodents. Ann. Zool. Fennici, 8:37-44.

Pucek, Z. and W.P.W. Lowe. 1975. Age criteria in small mammals. pp. 52-72 *in* Small Mammals: Their Productivity and Population Dynamics (F.B. Golley, K. Petrusewicz, and L. Ryszkowski, eds.). Cambridge Univ. Press, New York, xxv + 451 pp.

Ramsey, P.R. and L.A. Briese. 1971. Effects of immigrants on the spatial structure of a small mammal community. Acta Theriol., 16:191-202.

Randolph, P. 1973. Influence of environmental variability on land snail population properties. Ecology, 54:933-955.

Rasmussen, D.I. 1964. Blood group polymorphism and inbreeding in natural populations of the deer mouse *Peromyscus maniculatus*. Evolution, 18:219-229.

Redfield, J.A., M.J. Taitt, and C.J. Krebs. 1978a. Experimental alternatives of sex ratios in populations of *Microtus oregoni*, the creeping vole. J. Anim. Ecol., 47:55-70.

Redfield, J.A., M.J. Taitt, and C.J. Krebs. 1978b. Experimental manipulation of sex ratios of *Microtus townsendii*, a field vole. Canad. J. Zool., 56:17-27.

Rintamaa, D.L., P.A. Mazur, and S.H. Vessey. 1976. Reproduction during two annual cycles in a population of *Peromyscus leucopus noveboracensis*. J. Mamm., 57:593-595.

Robbins, R.J. 1977. An accurate, inexpensive, calibrated drinking tube. Lab. Anim. Sci., 27:1038-1039.

Rogers, J.G., Jr. and G.K. Beauchamp. 1974. Relationships among three criteria of puberty in *Peromyscus leucopus noveboracensis*. J. Mamm., 55:461-462.

Rogers, J.G., Jr. and G.K. Beauchamp. 1976. Influence of stimuli from populations of *Peromyscus leucopus* on maturation of young. J. Mamm., 57:320-330.

Rongstad, O.J. 1965. A life history study of thirteen lined ground squirrels in southern Wisconsin. J. Mamm., 46:76-87.

Rose, R.K. and M. Gaines. 1976. Levels of aggression in fluctuating populations of the prairie vole, Microtus ochrogaster, in eastern Kansas. J. Mamm., 57:43-57.

Rowe, F.P., E.J. Taylor, and A.H.J. Chudley. 1963. The numbers and movements of house mice (Mus musculus L.) in the vicinity of four corn ricks. J. Anim. Ecol., 32:87-97.

Rozin, P. 1974. The selection of foods by rats, humans, and other animals. Advances in the Study of Behavior, 6:21-76.

Rugh, R. 1968. The Mouse: Its Reproduction and Development. Burgess Publishing Co., Minneapolis, Minnesota, 430 pp.

Rusch, D.A. and W.G. Reeder. 1978. Population ecology of Alberta red squirrels. Ecology, 59:400-420.

Sadlier, R.M.F.S. 1965. The relationship between agonistic behavior and population changes in the deer mouse Peromyscus maniculatus (Wagner). J. Anim. Ecol., 34:331-352.

Sadlier, R.M.F.S., K.D. Casperson, and J. Harling. 1973. Intake and requirements of energy and protein for the breeding of wild deermice Peromyscus maniculatus. J. Reprod. Fertil. Suppl., 19:237-252.

Savidge, I. 1973. A stream as a barrier to homing in Peromyscus leucopus. J. Mamm., 54:982-984.

Schefler, W.C. 1969. Statistics for the Biological Sciences. Addison-Wesley Publishing Co., Reading, Massachusetts, 231 pp.

Schreiber, R.K. and J.H. Graves. 1977. Powerline corridors as possible barriers to the movements of small mammals. Amer. Midland Nat., 97:504-508.

Shannon, C.E. and W. Weaver. 1964. The Mathematical Theory of Communication. Univ. Illinois Press, Urbana, 125 pp.

Sheppe, W. 1965. Dispersal by swimming in Peromyscus leucopus. J. Mamm., 46:336-337.

Siegel, S. 1974. Flavor pre-exposure and "learned safety". J. Comp. Physiol. Psychol., 87:1078-1082.

Skryja, D.D. 1978. Reproductive inhibition in female cactus mice. (Peromyscus eremicus). J. Mamm., 59:543-550.

Slade, N.A. and D.F. Balph. 1974. Population ecology of Uinta ground squirrels. Ecology, 55:989-1003.

Smith, A.T. 1978. Comparative demography of pikas (*Ochotona*): effect of spatial and temporal age-specific mortality. Ecology, 59:133-139.

Smith, D.A. 1977. Effects of experimental botfly parasitism on gonad weights of *Peromyscus maniculatus*. J. Mamm., 58:679-681.

Smith, M.H., M.N. Manlove, and J. Joule. 1978. Spatial and temporal dynamics of the genetic organization of small mammal populations. pp. 99-113 *in* Populations of Small Mammals under Natural Conditions (D.P. Snyder, ed.). vol. 5, Special Publication Series, Pymatuning Laboratory of Ecology, Univ. of Pittsburgh.

Southwick, C.H. 1955. Regulatory mechanisms of house mouse populations: social behavior affecting litter survival. Ecology, 36:627-634.

Stebbins, L.L. 1977. Energy requirements during reproduction of *Peromyscus maniculatus*. Canad. J. Zool., 55:1701-1704.

Steiner, A.L. 1972. Mortality resulting from intraspecific fighting in some ground squirrel populations. J. Mamm., 53:601-603.

Stickel, L.F. 1946. The source of animals moving into a depopulated area. J. Mamm., 27:301-307.

Stickel, L.F. 1968. Home range and travels. pp. 373-411 *in* Biology of *Peromyscus* (Rodentia) (J.A. King, ed.). Special Publication No. 2, Amer. Soc. Mammalogists, xviii + 455 pp.

Stoddart, D.M. 1970. Individual range, dispersion, and dispersal in a population of water voles (*Arvicola terrestris* L.). J. Anim. Ecol., 39:403-425.

Strecker, R.L. 1954. Regulatory mechanisms in house mouse populations: the effect of limited food supply on an unconfined population. Ecology, 35:249-253.

Tamarin, R.H. 1977. Dispersal in island and mainland voles. Ecology, 58:1044-1054.

Tardif, R.R. and L. Gray. 1978. Feeding diversity of resident and immigrant *Peromyscus leucopus*. J. Mamm., 59:559-562.

Tarpy, R.M. and S.M. McIntosh. 1977. Generalized latent inhibition in taste aversion learning. Bull. Psychon. Soc., 10:379-381.

Tast, J. 1966. The root vole, *Microtus oeconomus* (Pallas) as an inhabitant of seasonally flooded land. Ann. Zool. Fennici, 3:127-171.

Terman, C.R. 1962. Spatial and homing consequences of the introduction of aliens into semi-natural populations of prairie deer mice. Ecology, 43:216-223.

Terman, C.R. 1965. A study of population growth and control exhibited in the laboratory by prairie deermice. Ecology, 46:890-895.

Terman, C.R. 1968. Population dynamics. pp. 412-450 in Biology of Peromyscus (Rodentia) (J.A. King, ed.). Special Publication No. 2, Amer. Soc. Mammalogists, xviii + 455 pp.

Terman, C.R. 1973. Recovery of reproductive function by prairie deermice (Peromyscus maniculatus bairdi) from asymptotic populations. Anim. Behav., 21:443-448.

Udvardy, M.D.F. 1969. Dynamic Zoogeography. Van Nostrand Reinhold Co., New York, xviii + 444 pp.

Van Valen, L. 1971. Group selection and the evolution of dispersal. Evolution, 25:591-598.

Van Vleck, D.B. 1968. Movements of Microtus pennsylvanicus in relation to depopulated areas. J. Mamm., 49:92-103.

Vessey, S.H. 1967. Effect of chloropromazine on aggression in laboratory populations of wild mice. Ecology, 48:367-376.

Vessey, S.H. and L.E. Mitchell. 1978. Immigration by white-footed mice (Peromyscus leucopus): absence of females. Ohio J. Sci., 78: 282-283.

Vestal, B.M. and J.J. Hellack. 1978. Comparison of neighbor recognition in two species of deer mice (Peromyscus). J. Mamm., 59:339-346.

Wecker, S.C. 1962. The effects of botfly parasitism on a local population of the white-footed mouse. Ecology, 43:561-565.

Whitaker, J.O., Jr. 1968. Parasites. pp. 254-311 in Biology of Peromyscus (Rodentia) (J.A. King, ed.). Special Publication No. 2, Amer. Soc. Mammalogists, xviii + 455 pp.

Wilson, E.O. 1975. Sociobiology: the New Synthesis. The Belknap Press of Harvard Univ. Press, Cambridge, Massachusetts, ix + 697 pp.

Yeaton, R.I. 1972. Social behavior and social organization in Richardson's ground squirrel (Spermophilus richardsonii) in Saskatchewan. J. Mamm., 53:139-147.