SOCIAL INTERACTIONS BETWEEN CONFINED JUVENILE AND ADULT PEROMYSCUS MANICULATUS BAIRDI: EFFECTS OF SOCIAL FACTORS ON JUVENILE SETTLEMENT AND GROWTH

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ABSTRACT

SOCIAL INTERACTIONS BETWEEN CONFINED JUVENILE AND ADULT *PEROMYSCUS MANICULATUS BAIRDI*: *EFFECTS OF SOCIAL FACTORS ON JUVENILE* SETTLEMENT AND GROWTH

By

John E. Enders

The objective of the present study was to investigate the social factors that may influence the outcomes of juvenile-adult interactions in *Peromyscus* *maniculatus* *bairdi* using field (3.8 m^2) or laboratory (1.2 m^2) enclosures. It was hypothesized that the sex of juveniles and the sex of adults and/or the reproductive stage of adult females would affect the settlement and growth rates of juveniles under two conditions of space quality.

A juvenile male or female was placed in an enclosure containing: (1) an adult male, (2) a nonlactating adult female, (3) a lactating female, or (4) no adult as a control. Five replications of each of the eight social treatment combinations were used in the field and laboratory experiments. The juveniles were free to interact with the adults over a four-day period. Juveniles could move through a two-way tunnel to an adjacent unoccupied enclosure, but adults could not, and all animals had access to nest boxes.

Juvenile settlement was evaluated experimentally by determining the propensity of juveniles: (1) to nest in enclosures occupied by adults, (2) to occupy the same nest with adults, and (3) to remain, during the nighttime active period, in enclosures occupied by adults. Significant differences among the social combinations were judged to

indicate relative effects of adults in limiting juvenile settlement. The differences between the initial and final juvenile weights were examined to determine the effects of the experimental treatments on juvenile growth.

The settlement of juvenile females, compared with juvenile males, was limited by nonlactating females. Settlement differences between the juvenile sexes were not significant when juveniles interacted with adult males or lactating females or encountered the control condition. Lactating females, compared with adult males, nonlactating females, and the control condition, limited the settlement of juvenile males. The settlement of juvenile females was not significantly different among the adult classes and the control. Similar outcomes of social interactions in free-ranging populations would result in nonlactating and lactating females, but not adult males, limiting the settlement of dispersing juveniles depending upon their sex.

The contradictions in the results of previous studies on Peromyscus (e.g., Healey, 1967) and the present research may be due to differences in the social behavior of different taxa and/or to differences in experimental designs since several biological determinants of social relationships were examined in the present investigation. Lactating P. m. bairdi exhibited maternal aggression, but adult males and nonlactating females were not aggressive. It is proposed that the settlement of juvenile male P. m. bairdi within populations is inversely related to the proportion of adult females that are lactating. On the other hand, juvenile female settlement may be inversely related to the population density of adult females irrespective of their reproductive condition.

Juvenile females, compared with juvenile males, had significantly lower growth rates when adult males were encountered. Differences in growth rates between male and female juveniles that interacted with nonlactating females or lactating females, or encountered the control condition, were nonsignificant. There were no significant differences in juvenile growth rates when the juvenile sexes were compared separately for the adult social factors, but control juvenile males gained significantly less weight than those males that interacted with adult males. These results may also reflect differences in the social behavior of different *Peromyscus* taxa. However, social interactions involving behaviors other than aggression, such as sexual behavior, may affect juvenile growth by altering juvenile activity and/or food intake, at least on a short-term basis.

The effects of the social factors on juvenile settlement were not similar under field and laboratory conditions possibly due to differences in the frequencies of behavioral interaction and/or avoidance. The effects of the social factors on growth rates were similar under the two conditions of space quality. But juveniles in the field experiment gained significantly more weight than the juveniles in the laboratory experiment.

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by

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INTRODUCTION

Dispersal, the movement of an organism from its natal site to another locality where breeding may occur (Howard, 1960), is being given increasing attention by ecologists studying small rodent populations. Sadleir (1965) and Healey (1967) indicated that *Peromyscus maniculatus austerus* immigrants were prevented from settling by aggressive adult males. However, in these studies, adult females were largely ignored, and the importance of the sex of the juveniles in determining the outcome of social interactions was not evaluated. Metzgar (1971) reported that the population density of adult female *P. leucopus* was inversely related to the number of juvenile females that settled within a local population, but males did not exhibit this relationship. The importance of different reproductive stages of the adult females was not evaluated by Metzgar, but differences in behavior towards strange juveniles may be expected because lactating *Peromyscus* commonly exhibit aggression or nest defense whereas nonlactating females typically do not (Eisenberg, 1963).

Dispersal in northern *Peromyscus* populations occurs during the breeding season (see Stickel, 1968). Dispersing juveniles may encounter and interact with any of three adult sex/reproductive-stage classes: males, nonlactating females, and lactating females. This investigation was designed to obtain quantitative measures of the outcome of these juvenile-adult interactions in *P. m. bairdi*, the prairie deer mouse. The objectives of this study were to determine if: (1) the sex of juveniles affects the outcome of social interactions, (2) the sex of adults and/or reproductive stage of adult females affects the outcome of social interactions, and (3) the outcome of social interactions are similar under field enclosure conditions and controlled laboratory conditions.

The impetus for this research stemmed from the fact that intraspecific social interaction has been hypothesized to lead to the regulation of small mammal populations (e.g., Chitty, 1967; Healey, 1967; and Metzgar, 1971). The basic argument in the proposed population regulation models is as follows. When an individual disperses, the local population density is decreased and the density of the population into which the individual immigrates is increased. So then, population densities can be dependent upon the behavioral interactions influencing the rates of departure from the natal site and settlement in a new site. Systematic study of the social behavior of small mammals is required in order to understand the role of behavioral mechanisms in dispersal and consequent population regulation.

Savidge (1970) operationally partitioned dispersal into three processes: (1) departure from the natal site, (2) crossing a barrier, usually unfamiliar space, and (3) settling in a new area. Each process can be investigated separately by controlling independent variables that may be important in determining the outcome of social behavior.

Savidge (1974) reported that juvenile P. m. bairdi crossed a barrier (an electrified grid connecting a natal cage with another cage) when the father crossed or if the mother was aggressive upon the birth of a subsequent litter. Nicholson (1941) suggested that P. leucopus ules

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males also attracted litters, and juveniles of other rodent species have been reported to depart from the natal area in response to aggressive mothers (Bradt, 1938, for *Castor canadensis* and Errington, 1939, for *Ondatra zibethica*).

Dispersing juvenile rodents, that have departed the natal site and are crossing unfamiliar space, encounter strange resident (*i.e.*, located in a home range) adults, interact, and may remain near the adult or continue to disperse. Social interaction between resident adults and dispersing juveniles has been reported to affect the settlement process in sciurids (*e.g.*, Drabek, 1973, for *Spermophilus richardsonii* and Carl 1971, for *S. undulatus*), *P. m. austerus* (Sadleir, 1965, and Healey, 1967), and *P. leucopus* (Metzgar, 1971). Detailed accounts of the social variables that may affect the outcomes of interactions in ground sciurids are available because this group is diurnal and easily observed in the field (*e.g.*, Bronson, 1964, and Betts, 1976). However, studies on the effects of encounters between strange adult and dispersing juvenile *Peromyscus* are rare. Such studies cannot be based on direct observation due to the difficulty in observing deer mice in the field. Rather, they should focus on the evaluation of the social factors that may influence spatial relationships while the mice are confined. When social conditions are controlled, the resultant spatial relationships can be inferred to be determined by social factors.

Social conditions were controlled in the present study by maintaining prairie deer mice in enclosures (1) under field conditions and (2) under controlled laboratory conditions where space quantity and complexity were decreased relative to the field conditions. The effects of social interaction upon juvenile settlement were evaluated experi

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experimentally by measuring the spatial relationships of juveniles and adults. Healey (1967) reported that aggressive male P. m. austerus retarded the growth rate of juveniles in field and laboratory experiments. The growth rates of all juveniles in the present investigation were measured in an attempt to reexamine and expand upon these findings. Also, several other measures (e.g., activity and wounding) were taken.

Literature Review

Dispersal is a poorly understood demographic factor in small rodent populations. Much of the lack of understanding can be attributed to the difficulty in studying dispersal in free-ranging populations (Myers and Krebs, 1971). Also, dispersal is a dynamic process; a variety of biotic and abiotic factors may act alone or in combination to determine an observed dispersal rate or pattern (Lidicker, 1975). This literature review is restricted, for the most part, to pertinent information of the intraspecific social factors governing the dispersal process of settlement. The review is organized in the following fashion. Firstly, a general definition of social relationships and determinants of social relationships will be given, and secondly, the social relationships that may affect the settlement of juvenile rodents will be presented. Thirdly, hypotheses concerning dispersal in small mammals will be discussed, but only those dealing with the settlement and growth rates of dispersing juveniles will be analyzed in detail. Fourthly, a general presentation of evolutionary considerations will be given followed by, five, a general summary of the predictions of the outcomes of social interactions between strange juveniles and adults.

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Social Relationships

When two individuals come together and react to one another, their behavior is no longer independent, and a social relationship may be formed (Scott, 1973). Scott developed the concept of social relationship to promote the investigation of social organization in group-living species such as primates. The same conceptual framework may be used to study social encounters between strange juvenile and adult *Peromyscus* even though this genus usually does not occur in groups other than a monogamous pair and their offspring, at least during the breeding season (Terman, 1968). The outcome of a social encounter, in terms of settlement and subsequent use of space by the juvenile, may be determined by the factors that determine the formation of a social relationship.

Determinants of Social Relationships

According to Scott (1973), two components are necessary for the differentiation of behavior into a social relationship. Firstly, animals must have ability to discriminate between individuals, and secondly, behavioral patterns must be present that can be modified by experiential and biological factors.

Individual recognition in *Peromyscus* is probably accomplished by using a variety of cues, and this genus has well developed receptor organs for auditory, tactile, visual, and olfactory stimuli (King, 1968a). Pair bonding (Howard, 1949) and stable dominance hierarchies over time (Sadleir, 1970) provide evidence for the existence of individual recognition in *Peromyscus*.

Experiential factors may be subdivided into two categories: (1) early experience and (2) experience with an area of familiarity with another animal. The amount and quality of infantile stimulation has been shown to affect behavior at a later developmental stage in rodents (Levine et al., 1967), but the processes and mechanisms associated with the effects of early experience are not known (Russell, 1971). Terman (1963) reported that P. m. bairdi, raised in isolation, were less inclined to be social than were mice raised in social groups. An understanding of the preweanling biotic and abiotic environments is required prior to evaluating the significance of early experience in the subsequent social behavior of Peromyscus. However, the available evidence indicates that early experience must be controlled in experimental studies of social behavior.

The outcome of social encounters in Peromyscus, and other rodents, can depend upon the location of the encounter and the degree of familiarity between animals. An animal in familiar surroundings usually becomes dominant over an intruder, if a dominance-subordinant relationship ensues (Eisenberg, 1962, and Grant, 1972), and mice tend to exhibit less aggression towards familiar conspecifics than towards strange conspecifics (Poole and Morgan, 1975). These concepts are integral to the settlement process of juveniles for several reasons. The activity of adult Peromyscus is usually restricted to a localized area or home range; it has been claimed that adults are familiar with the area encompassing their home range (Furrer, 1973). Secondly, the encounter between a dispersing juvenile and strange resident adult typically takes place in the adult's home range. Finally, agonistic behavior or overt aggression (fighting) involved in the establishment of the dominance-subordinant relationship may force the juvenile to leave the presence of the adult and continue to disperse. Two points must be considered prior to accepting the apparent role of dominance-subordinant relationships, as determined by agonistic behavior, in influencing juvenile settlement (Healey, 1967): (1) there is no evidence of territoriality or defense of mutually exclusive areas in Peromyscus (Hill, 1970) and (2) behaviors other than those that are agonistic may be involved in the establishment of a social relationship. The latter point will be discussed in detail in the section on the types of social relationships that may influence juvenile settlement. Agonistic behavior, as used in this paper, refers to any behavior which is connected with a contest or conflict between two conspecifics whether fighting, escaping, or "freezing" (Scott, 1972).

Biological factors may be subdivided into four categories: (1) genetic constitution, (2) age, (3) sex, and (4) reproductive condition/physiological state. A genetic basis for behavioral differences in Peromyscus, beyond species and subspecies comparisons of habitat selection and social behavior (Harris, 1952, and see Eisenberg, 1968), has not been reported. Male (Healey, 1967) and lactating female (Savidge, 1974) P. maniculatus have been found to vary markedly in aggressive tendencies. These reported differences may have a genetic basis, but selection experiments are required in order to determine heritability. Randomization of experimental animals can be used to avoid biasing results in studies on social behavior in which possible genetic differences are of no interest.

Age can be an important factor influencing social behavior. In general, adult mammals are usually dominant over immatures. Grant

(1970) stated that body size, which is directly related to age in most rodents including P. maniculatus (Dice, 1932 and 1936), is a reliable correlate of dominance in agonistic encounters. Field studies have indicated that maturing rodents undergo gradual changes in responsiveness to conspecifics and vice versa, which in turn, cause changes in social relationships (e.g., Barash, 1973, for Marmota olympus and Betts, 1976, for S. columbianus). These changes, while certainly correlated with growth and increased body size, are also correlated with physiological changes associated with the onset of sexual maturity (Poole and Morgan, 1975). There is a need for detailed study of the development of social behavior in Peromyscus as was done for Microtus agrestis (Wilson, 1973). Until this information is available, age classes should be standardized in studies examining other determinants of social behavior. This procedure would result in a reduction of confounding variation due to changes in age-specific responsiveness of the experimental animals.

The sex of mammals is of paramount importance in the determination of their social behavior and social relationships. Adult male Peromyscus have been claimed to be more agonistic than adult females, especially toward other males, although both sexes are capable of the same aggressive behavioral patterns (Eisenberg, 1968). However, only a few species have been critically examined. It is interesting to note that both male and female P. polionotus, P. leucopus, and P. m. bairdi 28-day olds were similarly agonistic towards Microtus weanlings (Baenninger, 1973). Therefore, differences in levels of agonistic behavior may appear as deer mice mature to adults.

The social relationships of resident adult and dispersing juvenile *Peromyscus* females have been critically examined in only one study (Metzgar, 1971, for *P. leucopus*), and repulsion of juvenile females was reported. Females have been largely ignored in other investigations of small mammal dispersal in which behavioral mechanisms were examined (Krebs, 1970, and Myers and Krebs, 1971). A systematic study of the effects of social factors on the settlement patterns of dispersing juveniles should evaluate differences due to the sexes of the interacting juvenile-adult combinations.

Changes in reproductive condition and concomitant physiological state of mammals give rise to changes in social relationships. Male *Peromyscus* remain in breeding condition throughout the breeding season and have been reported to be aggressive during this time (Sadleir, 1965, and Healey, 1967, for *P. m. austerus*), probably due to high testosterone levels (Bronson and Desjardins, 1971). On the other hand, female *Peromyscus* exhibit behavioral changes within a single breeding season. Prairie deer mice come into estrus about every three days upon exposure to males (Bronson and Marsden, 1964), and the behavior of females may shift in response to changes of the estrus cycle. For example, Payne and Swanson (1970) found that female *Mesocricetus aruatus* were less agonistic towards male conspecifics during peak estrus compared to other stages in the cycle. Maternal aggression can be elicited by the presence of the offspring and some threatening agent (Moyer, 1971). King (1958) and Scudder *et al*. (1967) reported that lactating *P. m. bairdi* exhibit nest defense, and female *Meriones unguiculatus* were found to greatly increase aggressiveness following parturition (Thiessen, 1973). Other rodent females, in the lactation stage, have been inferred to be aggressive towards conspecifics (Blair, 1942, for _Tamias striatus_ and Broadbooks, 1970, for _Eutamias amoenus_). The effects of nonlactation and lactation stages on juvenile-adult social relationships between strange animals have not been critically examined in _Peromyscus_, but differences in juvenile settlement may be related to these different adult reproductive stages.

Social Relationships Affecting the Settlement of Juvenile Rodents

The spatial organization of individuals in _Peromyscus_ populations has been described in capture-recapture and nest box studies. In general, the movement of resident and probably breeding adults is localized within a home range where the animal normally travels in pursuit of its routine activities. Home ranges are usually maintained for the life of the individual, but some adults leave established home ranges. The measured spatial arrangement of home ranges is variable and seems to depend upon the taxonomic groups being studied, geographical location, and possibly the methods used in the measurement. During the nonbreeding season, the exclusiveness of home ranges decreases (see Stickel, 1968, and Terman, 1968). The mechanisms leading to the exclusiveness of home ranges, the formation of social relationships, and the incorporation or settlement of juveniles into the matrix of home ranges is unclear. However, Hill (1970) found that neither male nor female _P. m. bairdi_ and _P. leucopus_ defended a familiar area from same or opposite-sex conspecifics.

There are many types of social relationships that can be formed depending upon the experiential and biological characteristics of the animals involved in interactions (Scott, 1973). Two relationships

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between strange resident adults and dispersing juveniles are central to the settlement process. Firstly, dominance-subordinate relationships may be established. However, there are serious methodological difficulties with the dominance concept (see Richards, 1974, for review). Several definitions of dominance have been proposed, but direct observation of interacting animals in order to obtain the required measurements is impossible for Peromyscus in the field.

That dominance in murid rodents is established by agonistic behavior is well known (e.g., Poole and Morgan, 1973, and Bovet, 1972), and dominance hierarchies resulting from agonistic encounters have been reported for Peromyscus (Sadleir, 1970). The works of Sadleir (1965) and Healey (1967) are often cited to indicate that aggressive interaction is virtually universal in altering the settlement pattern of juveniles (e.g., Barash, 1977). It may be submitted that agonistic interaction and subsequent escape of the juvenile may be sufficient for influencing the settlement of juveniles, but it is not necessary. Orr (1959) and Terman (1962) reported that Peromyscus simply avoid conspecifics upon encounters, though it was not known if elements of agonistic behavior were involved in the avoidance. Also, it has been found that subordinate Peromyscus frequently nest with dominants (Hill, 1970). Hence, subordinate individuals in free-ranging populations may not necessarily leave the presence of dominant individuals.

Sexual relationships are the second type of relationship that may be involved in the settlement process. In the absence of agonistic interaction and/or avoidance, opposite sex individuals may be attracted. That juvenile Peromyscus usually disperse at about the time they attain sexual maturity (Howard, 1949, for P. m. bairdi, and see Blair, 1953, and Stickel, 1968, for other species) suggests that sexual behavior may be important in determining the outcome of social encounters as they relate to settlement.

The social conditions influencing social relationships and consequent settlement patterns in dispersing deer mice are poorly understood. The lack of understanding can be attributed to the failure of past workers to consider the factors that determine the formation of social relationships. Sex and reproductive condition are important factors in determining social relationships and can be manipulated in a systematic study on the social factors influencing settlement in juvenile deer mice. Other factors can be standardized or randomized.

Hypotheses Concerning Dispersal in Small Rodents

An array of proposals concerning the causes and effects of social behavior in the dispersal phenomenon and subsequent population and individual consequences have been published. Howard (1949) proposed that dispersal ability enables a species to reinvade depopulated areas or newly created favorable habitats. Further, a genetically determined tendency to disperse was suggested by Howard (1960). That is, some vertebrates are claimed to have an inherited propensity to disperse and avoid readily available and suitable habitat to enter novel, and probably unfavorable, areas where their chances of survival are potentially low. Presumably, these individuals disperse irrespective of the social conditions in the natal and settlement sites. Conversely, other individuals are claimed to disperse due to social and physical parameters such as mate selection, territoriality, parental ejection, or lack of suitable homesites. According to Howard, the innate dispersers are often sacrificed for the "good" of the species because they facilitate gene flow, enlarge the range of the species, and permit the species to maintain a discontinuous distribution and reinvade depopulated areas. This proposal necessitates the acceptance of group selection. However, the role of group selection cannot be supported by current evolutionary theory (Williams, 1966).

Chitty (1967) hypothesized that selection for aggressive dominant individuals increases as population density becomes higher, and that dispersal of genetically subordinant individuals is greatest at high population densities. Myers and Krebs (1971) found genetic differences between dispersed and resident *Microtus*, but these authors could not determine whether the different genes caused different levels of aggression. Further, no marked differences in aggressive behavior between dispersing and resident male *Microtus* were found, though it was suggested that dispersing *M. pennsylvaticus* males were more aggressive than resident males (Myers and Krebs, 1971). Other lines of contradictory evidence may be used to argue against acceptance of Chitty's idea concerning the population density-dispersal and population density-aggression relationships. Myers and Krebs (1971) and Rose and Gaines (1976) found that dispersal in *Microtus* populations was not greatest during periods of highest population densities. However, Joule and Cameron (1975) reported that *Sigmodon* and *Reithrodontomys* dispersal was positively correlated with population densities, though the causative mechanisms were not evaluated in their study. Lidicker (1973, for *M. californicus*) and Rose and Gaines (1976, for *M. ochrogaster*) reported that wounding, and therefore aggression, was not greatest during peak population densities, but seemed to vary with seasonal changes. In

conflict with these reports, Krebs (1970) observed high levels of aggression in laboratory encounters between wild-caught male *M. ochrogaster* and *M. pennsylvanicus* captured during the period of peak population density, and Conley (1976) described similar findings for male and female *M. longicaudus*. Also, Christian (1971) noted that wounding in male *M. pennsylvanicus* was positively correlated to population density. Clearly, the relationship between aggression and population density has not been firmly established and requires future study.

The above investigations were designed to examine the cause and effect of dispersal at the population level. The primary purpose of these studies was to describe attributes of dispersing individuals, establish the relationships between population density-dispersal-aggression correlates, or to explore alternative relationships between dispersal and environmental components. Another line of research has been directed towards specific questions concerning the social relationships between resident adults and dispersing juveniles in reference to the process of juvenile settlement within local populations. These investigations have a direct bearing on the present study and will be analyzed in detail.

Sadleir (1965) proposed that resident adult *P. m. austerus* males were aggressive during the breeding season and inhibited the survival of juvenile conspecifics. Healey (1967) confirmed the claim that male *P. m. austerus* in breeding condition were aggressive. This author also reported that the growth rates of juveniles were retarded due to social interaction with resident adult males in confined laboratory enclosures. In addition, the growth rates and survival (*i.e.*, remaining within an

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area) of released juveniles were lower in field plots containing aggressive adult males compared to those juveniles released onto plots containing docile males. Healey proposed that local *Peromyscus* populations were regulated by aggressive adult males forcing surplus juveniles to settle elsewhere.

Flowerdew (1974) removed adult male *Apodemus sylvaticus* from a study plot and found that the survival of subadults and juveniles was significantly better compared to a control plot on which adults were allowed to remain. Further, laboratory experiments indicated that some aggressive adult males decreased juvenile growth rates and killed juveniles, though the supportive evidence was weak. This author concluded that population control in *Apodemus* was similar to that claimed for *Peromyscus* by Healey (1967).

Metzgar (1971) hypothesized that *P. leucopus* populations are regulated by intraspecific behavioral interactions. Juveniles were released onto a study plot containing resident adults and settled in areas unoccupied by adults of the same sex. When resident adult female density increased, female immigrants were less likely to settle, but males did not exhibit this pattern. Metzgar (1971) suggested that social interaction between females results in more repulsion of juveniles compared to interaction between males. That is, resident females limit the settlement of transient females, but resident males do not limit the settlement of transient males.

The conflicting conclusions in the above studies can be attributed to two factors. First, the social organizations of the different taxa may be different, although there is no experimental verification. Healey (1967) suggested that *P. m. austerus* are organized into units of

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familiar animals which repulse the settlement of strange deer mice. Brown (1969) suggested that A. sylvaticus occur in groups in which a single dominant male is surrounded by a few females and several immatures. Dominant males have been found to control the activity of group members in Apodemus (Bovet, 1972) and other murids (Crowcroft and Rowe, 1962, for Mus and Calhoun, 1963, for Rattus), but aggression within groups is low. Strange conspecifics are repulsed from organized colonies of Rattus (Calhoun, 1963). Myton (1974) recently reported that P. leucopus are arranged into "family groups" containing a single adult female, several males, and a number of juveniles. However, the relatedness of these wood mice was not known.

Secondly, the conclusions may have been influenced by the experimental designs. The field experiments suffered from a lack of control of test animals. Adults and juveniles disappeared for unknown reasons, effects of social interaction between and among resident adults and immigrating juveniles could not be eliminated, and Healey (1967) measured growth rates only on those juveniles that remained on the study site and were recaptured. Also, some docile males became aggressive and some aggressive males became docile during Healey's (1967) study, but since results from these animals were not included in his analysis, the conclusions were not influenced.

The functional significance of the effects of adult male P. m. austerus on juvenile growth is not clear primarily because the cause-effect relationship between aggression and delayed maturation in rodents is not understood. The physiological mechanism responsible for the inhibition of juvenile growth and possible retardation of sexual maturation is often postulated to be the pituitary-adrenocortical-gonadal triad

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which responds to stress stemming from social conditions (King, 1973). However, the supportive evidence for the role of this physiological mechanism has been obtained primarily from laboratory experiments where animals were exposed to supernormal social stresses such as extremely high cage population densities, long periods of exposure to social treatments, and high levels of aggression compounded by severe confinement (see Christian _et_ _al_., 1965). A second and more general explanation may be that short-term adult-juvenile interactions affect juvenile growth by altering the activity, energy expenditure and/or food intake of juveniles. These alterations could be mediated directly by social interactions, involving aggression or some other behavior, if adults restrict juvenile movement and the amount of food juveniles contact and eat and/or somehow cause differences in activity and therefore energy expenditure of the juveniles.

Data from laboratory studies do not provide conclusive support of either the existence of inhibition or the specific social correlates of inhibition that can be extrapolated to free-ranging populations. Terman and Gardner (1970) investigated the effect of cage population density on the growth of _P_. _m_. _bairdi_. Only a few significant body weight differences were noted in prairie deer mice that were 40, 60, 80, or 100 days of age. These differences among males or females were either due to age differences or could not be explained in relation to any independent variable in the experimental design. In a recent study, Thomas and Terman (1975) reported that male, but not female, _P_. _m_. _bairdi_ had significantly higher body weights at 100 to 140 days of age when reared with bisexual pairs than males reared in populations of four bisexual pairs and offspring. Whether communal nursing, social

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interaction, or some other population experience caused the difference in growth was not known.

The laboratory portions of the studies by Healey (1967) and Flowerdew (1974) can be severely criticized because the juveniles could not escape the presence of aggressive adults, as is the case for free-ranging populations if open space is available. There is a need to investigate the effects of adult-juvenile behavioral interaction on juvenile growth rates in conditions where the juvenile can escape the presence of the adult.

Adult females were largely ignored in the studies of Sadleir (1965), Healey (1967), and Flowerdew (1974). However, pilot studies conducted by Healey (cited in Metzgar, 1971, and Fordham, 1974) indicated that aggressive female *P*. *m*. *austerus* determined the number of immigrating females that settled in an area. Metzgar's (1971) work on *P*. *leucopus* supports this tentative finding for females, but general conclusions concerning females must be tempered until an evaluation of the role of reproductive stage (*i*.*e*., nonlactation *vs*. lactation stages) in determining the outcome of social encounters is conducted.

Finally, the sexes of juveniles in the research conducted by Sadleir (1965), Healey (1967), and Flowerdew (1974) were not reported, but Metzgar (1974) found differences in the settlement patterns of juvenile males and females. The juveniles used by Healey were sexually immature, but Metzgar used 40 to 60 day-old young. Clark (1938) reported that *P*. *leucopus* go into their first estrus at about 46 days of age. Therefore, it is possible that Metzgar's deer mice were sexually mature. In light of the role of sex in determining social relationships, ready acceptance of generalizations on the importance of resident

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adults in affecting dispersing juveniles is premature until a quantitative evaluation of the effects of the sex of juveniles has been made.

Evolution

Dispersal, at times, results in animals leaving an optimum area and entering a different area in time and space in which the probability of mortality is high (e.g., Carl, 1971). Some authors have indicated that dispersing individuals are sacrificed for the "good" of the species since ranges may be expanded and/or population regulation may be effected (Howard, 1960, and Christian, 1970). Van Valen (1971) verified that group selection could lead to dispersal by using a computer simulation with the assumptions of haploid organisms and asexual reproduction. However, there is no aspect of mammalian dispersal that cannot be explained on the basis of individual selection.

Natural selection is the nonrandom differential perpetuation of varying gene frequencies (Mettler and Gregg, 1969). That is, genes that enhance adaptiveness by increasing the probability of reproductive success of the individual are selected for over time so that their frequencies increase. Lidicker (1962 and 1975) proposed that the probability of reproductive success of individuals that disperse from a population before the habitat becomes saturated with conspecifics could be increased due to four advantages: (1) dispersers have an increased opportunity for mating because they contact more potential mates, (2) with outbreeding there is an increased chance for producing favorable genetic recombinants, (3) dispersers may avoid population crashes and predator buildups, and (4) during periods of high population density remaining resources become scattered and resource utilization becomes

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inefficient; dispersers avoid this inefficiency. These proposed advantages are logical and deserve experimental evaluation. However, the topic of the present research is the social factors affecting dispersal within a population. The basic premise I have taken is that the processes of dispersal (departure from the natal site, crossing unfamiliar space, and settlement) occur when individuals are likely to increase their inclusive fitness. This increase can be achieved by increasing the probability of (1) a disperser's reproductive success and/or (2) the reproductive success of animals related to a dispersing individual (Hamilton, 1964, and Murray, 1967). The following presentation of evolutionary considerations will be divided into two sections: (1) departure from the natal site and (2) crossing unfamiliar space and settlement.

Departure From the Natal Site

Most *P. m. bairdi* (Howard, 1949, and Dice and Howard, 1951) and other rodents (*e.g.*, Drabek, 1970, for *S. tereticaudus*, Rongstad, 1965, for *S. tridecemlineatus*, and Layne, 1954, for *Tamias striatus*) disperse as juveniles. However, fall-born *P. m. bairdi* litters remain with their parents until the following spring (Howard, 1949). Some sciurids do not disperse until they are two or three years old (Barash, 1974). On the other hand, King (1955) reported that *Cynomys ludovicianus* juveniles do not disperse, but rather the parents do. Further, 38 per cent of the juvenile females and 28 per cent of the juvenile male *P. m. bairdi* studied by Howard (1949) did not disperse (Dice and Howard, 1951). Similar contradictory reports can be found for other mammalian orders (*e.g.*, Ewer, 1973, for carnivores).

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Differences between taxa can be partially attributed to different evolutionary histories. Barash (1974) used the comparative approach to ascertain behavioral-environmental correlates of dispersal in three species of *Marmota*. *Marmota monax* live at low elevations and disperse during their first year; *M. flaviventris* occur at medium elevations and disperse as one-year olds; *M. olympus* are found at high elevations and disperse as two-year olds. The food supplies of the local environment vary inversely with elevation, but the age to sexual maturity vary directly with elevation. Barash suggested that dispersal was delayed at higher elevations in order to allow the young to attain adult body size prior to dispersing. The social determinant of dispersal seemed to be aggressive mothers, but females exhibited little aggression towards their maturing young until they attained adult body size. According to Barash, these mother-offspring relationships would increase the probability of the reproductive success of dispersing juveniles, which in turn, would increase the inclusive fitness of the parental adults. While the suggestions above are speculative and require much more supportive data before they can be accepted, the systematic comparative approach has great potential in identifying salient features of the environment that may exert selective pressures on the dispersal processes. It is apparent that the evolutionary histories of taxa must be considered prior to making generalizations across groups.

Agonistic interaction between the female parent and weaned offspring upon the birth of a subsequent litter has been reported or suggested to cause immatures to depart the natal site in *P. m. bairdi* (Savidge, 1974), *C. canadensis* (Bradt, 1938), *O. zibethica* (Errington, 1939), and sciurids (*e.g.*, Michener and Michener, 1973, and Smith,

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1968). The situation where a female actively expels his offspring from a suitable living space seems paradoxical.

According to Trivers (1974), parental-offspring conflict is to be expected in sexually reproducing species. Parents are assumed to expend energy and incur physical risk so as to maximize the number of offspring that survive and reproduce. However, individual offspring can be thought of as trying to maximize their reproductive success by attempting to secure more investment than the parent is selected to give. It must be understood that the parent and offspring are related by one-half, as are siblings. Any increase in the parental investment for one genetically (i.e., a genetically determined behavior that elicits more maternal care than is necessary) favored offspring will tend to decrease the number of siblings that survive, and consequently reduce the number of like genes (in reference to the favored offspring) located in the siblings. Then, the gene in the favored offspring will be selected against, if it extracts too great a cost from the parent, even if it confers some benefit on the favored offspring.

Benefit and cost are defined by potential reproductive success or fitness (Hamilton, 1964). In order for an act (behavior governed by a gene) to be selected for, the benefit/cost ratio times the probability that the recipient of a favorable act has the gene must be greater than one. Specifically, for an act to have survival value, its benefit/cost ratio must be larger than the inverse of the actors degree of relatedness to the recipient.

As young mammals grow they become more expensive for the mother in terms of the energetic cost of milk production and in terms of the delay in producing another litter of offspring. Trivers argued that as

offspring age they benefit less from nursing and become increasingly capable of independency, but the cost to the mother increases as time goes on. If cost and benefit are expressed in the same units, the cost to the mother will exceed the benefit to her young at some point. Then the inclusive fitness of the mother will be reduced. However, the offspring should attempt to nurse until the cost to the mother is more than twice the benefit to himself because he is related to future sibs by one-half. So then, at some period there is a conflict between individual maximization of the mother's and offspring's inclusive fitnesses.

The mother could be expected to expel her offspring when the benefit/cost ratio of the act to the mother exceeds the inverse of her relatedness to her offspring, if production of another litter is possible. It follows that the aggressive interaction observed between females and their offspring which results in the departure of offspring from the natal site can be explained on the basis of the inclusive fitnesses of the mother and the future litters of offspring.

The above discussion was not meant to pertain to all rodent species. King (1955) reported that C. ludovicianus parents were not aggressive towards their offspring, and usually deserted weaned litters. Adults established new burrows in available open areas, and the young usually remained in central areas of the colony where predation was lower compared to peripheral areas. Layne (1954) suggested that T. striatus litters gradually wander away from the natal area. The mechanisms associated with this "passive" departure were not stated, but the possibility exists that exploratory behavior, under selective control, can lead to departure from the natal area. This tentative suggestion has been investigated. Some *P. m. bairdi* juveniles do not leave the natal area (Dice and Howard, 1951). Failure of these juveniles to depart the natal area may have been due to disappearance of the mothers of variation in the propensity of females to be aggressive towards their offspring as was reported by Savidge (1974).

A final point to consider for departure from the natal site is that intensive inbreeding could lead to a decrease in reproductive performance due to decreased heterozygosity (Crow and Kimura, 1970). A precise measure of inbreeding has not been published for free-ranging small rodent populations, though Howard (1949) estimated that 4 to 10 per cent of the litters produced during his study were from parent-offspring or sib matings. This author pointed out that juvenile dispersal from the natal site would reduce the probability of parent-offspring matings. The trend for female deer mice to mature earlier than males may serve to reduce breeding among litter mates (see Layne, 1968), if litters in free-ranging populations disperse together as was found by Savidge (1974) in a laboratory study. Given the proposed selective advantages of juveniles that leave the natal site, other factors must be operating to limit the dispersal of juveniles because Rasmussen (1964), using Howard's data for *P. m. bairdi*, estimated the size of interbreeding units within continuous habitat to be 12 to 99 individuals.

Crossing Unfamiliar Space and Settlement

It is often stated that dispersing or wandering rodents have a high probability of death (*e.g.*, Lidicker, 1975), but the documentation for this claim comes from field studies where emigration from the study plot and realized mortality cannot be distinguished (e.g., Watts, 1969, and Myton, 1974). Metzgar (1967) and Ambrose (1972) reported that experience within an area was a significant factor in avoiding predation under controlled laboratory conditions for P. leucopus and M. pennsylvanicus, respectively. Therefore, predation is probably relatively high for juveniles wandering through unfamiliar terrain.

Presumably, the chance of reproductive success is inversely related to the time during which the individual continues to wander in unfamiliar terrain. Unfortunately, this time dependent measure cannot be obtained for small mammals in free-ranging populations, and various indices of dispersal distance have been used instead. Reports range from anecdotal accounts to detailed analyses. For example, Layne (1954) simply suggested that young T. striatus left their natal woodlot; whereas Godfrey (1953) reported that only one of 21 M. pennsylvanicus, first captured as immatures, was taken more than about 27 m from the initial capture point when mature. Howard (1949) was able to determine the breeding site of 155 P. m. bairdi out of 675 individuals for whom the birthplace was also known. One hundred and nineteen individuals bred within about 152 m of their natal site. The remaining mice moved up to about 1000 m from their birthplace. Males tended to move further than females (Dice and Howard, 1951).

Murray (1967) proposed that the relative dominance of individuals in procuring a breeding site determine dispersal distances in vertebrates. A breeding site can be considered to be an area containing the necessary habitat features such as suitable space, food, nesting sites, predator escape routes, etc. According to Murray, selection will favor individuals that aggressively procure breeding sites, but move away from dominant animals, even if continued dispersal entails a risk to the individual. The probability of reproductive success of the subordinant animal is maximized by leaving the presence of the dominant; to stay and "fight to the death" would reduce its chances of reproductive success to zero.

There are two shortcomings in this proposal pertaining to dispersal in P. m. bairdi. Firstly, the assumption that aggressive interaction is the only behavior involved in the establishment of social relationships may not be valid. Secondly, as was the case in past studies of the settlement process in juvenile Peromyscus, failure to consider the role of the biological determinants of social behavior and consequent social relationships may result in inaccurate cause and effect explanations of the settlement process in juveniles. However, the conceptual framework of Murray's proposal can be used to formulate summary predictions concerning the potential outcomes of social interaction between a resident adult and a dispersing juvenile. The following summary predictions are jointly based on previous studies and considerations of evolutionary arguments. In each case the resident adult is not the parent of the strange, dispersing juvenile and is in breeding condition.

Summary

Adult Male-Juvenile

The works of Sadleir (1965) and Healey (1967) lead to the prediction that an adult male should aggressively repulse all juveniles. The ultimate reasons for this prediction follow the argument of Murray (1967). On the other hand, Metzgar's (1971) findings suggest that juvenile females should settle near adult males, but juvenile males should not. The ultimate reasons for this prediction may be that a sexual relationship is formed between adult males and juvenile females and juvenile males are repulsed. Another possibility is that juvenile males should avoid adult males and continue to disperse until they encounter mates.

Adult Nonlactating Female-Juvenile

Healey (1967) largely ignored adult females because preliminary laboratory experiments indicated that they were not aggressive and did not affect juvenile survival or growth rates. The work of Metzgar (1971) leads to the prediction that juvenile males settle near nonlactating females, but juvenile females do not. The ultimate reason for this prediction could be that a sexual relationship is formed between nonlactating females and juvenile males, and juvenile females are repulsed. However, there is little evidence to indicate that nonlactating females are aggressive. Another possibility is that juvenile females should avoid nonlactating females and continue to disperse until they encounter a mate.

Lactating Female-Juvenile

Social interactions between these social combinations have not been previously examined. A tentative prediction, based on the occurrence of nest defense and maternal aggression in *Peromyscus*, is that both male and female juveniles should be repulsed (King, 1958, and Scudder *et al.*, 1967). The ultimate reason for this prediction may be that lactating females maintain a resource supply for milk production and/or for the offspring as they become independent. However, the area

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over which the nest defense is extended is not known. Also, the aggressiveness of female Peromyscus with litters appears to differ among taxonomic groups (Eisenberg, 1968).

The Purpose of This Study

The purpose of the present study was to obtain quantitative measures of the outcome of social interactions between an adult P. m. bairdi and a strange juvenile conspecific. This investigation was designed to control or randomize the confounding variables of experience, genetic constitution, age, and population density. The sex of juveniles and the sex and/or reproductive stage of adults were used as the independent variables. Experiments were repeated under two environmental conditions -- field-enclosure and laboratory -- in order to determine if the social variables had the same relative influence in two conditions of space quality.

A dispersing juvenile in a free-ranging population may encounter a strange adult and remain with that adult or continue dispersing. The adult presumably remains in its home range. This condition was simulated by placing a juvenile male or female in an enclosure containing an adult male, a nonlactating and nonpregnant adult female, a lactating female with her litter, or no adult as a control. Juveniles could move through a two-way tunnel to an adjacent unoccupied enclosure, but the tunnels were designed to prevent the passage of adults. All deer mice had access to nest boxes.

The effects of social interaction upon juvenile settlement were evaluated experimentally by measuring the spatial relationships of juveniles and adults within the enclosures. Since it has been claimed that he growth

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the growth rates of juvenile *Peromyscus* are retarded by some adults, the weight changes of juveniles were measured. Also, several other measures were taken (*e.g.*, activity and wounding) during this study. The social conditions were altered independently. Therefore, the relative differences in the dependent variables in respect to the juvenile sexes and in respect to the adult classes could be determined. It was expected that the outcome of juvenile-adult social interactions would be affected by the biological classes of interacting animals.

The present investigation evaluated the following working hypotheses concerning the outcomes of juvenile-adult social interactions in *P. m. bairdi*:

(1) The sex of juveniles and the sex of adults and/or the reproductive stage of adult females affects juvenile settlement.

(2) The sex of juveniles and the sex of adults and/or the reproductive stage of adult females affects juvenile growth.

(3) The relative effects of the biological classes will be similar under field-enclosure conditions and controlled laboratory conditions.

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METHODS

Design

The experiment required a male or female juvenile to encounter: (1) an adult male, (2) an adult female that was neither lactating nor pregnant, hereafter referred to as a nonlactating female, (3) a lactating female and her litter, or (4) no adult as a control. Experiments were repeated using field and laboratory enclosures with five replications for each treatment combination (*i*.*e*., location x juvenile x adult, Table 1). Overall, a total of 80 juveniles and 60 adults were used. Juveniles were allowed to interact with adults over four consecutive nights. Therefore, the total number of test nights was 320.

Table 1. The experimental design used in this study.

Location:	Field Enclosure		Laboratory Enclosure	
Adult	Juvenile			
	Male	Female	Male	Female
Male	5	5	5	5
Nonlactating Female	5	5	5	5
Lactating Female	5	5	5	5
Control (No Adult)	5	5	5	5

Experimental Animals

The prairie deer mouse, *Peromyscus maniculatus bairdi*, was chosen as the experimental animal for the following reasons:

(1) A vast amount of background information is available for this genus and especially this species (King, 1968b).

(2) Previous workers have described dispersal in free-ranging populations and have evaluated the influence of social interaction on the dispersal phenomenon in this genus (Howard, 1949; Dice and Howard, 1951; Healey, 1967; Metzgar, 1971; and Savidge, 1974).

(3) This species is easily maintained in captivity.

All mice used in this study were the F_1, F_2, or F_3 generations of wild caught parental stock collected in the vicinity of East Lansing and Ann Arbor, Michigan. While in the colony, mice received food (Wayne Lab-Blox) and water *ad libitum*; wood shavings served as bedding. Mice used in the field tests were maintained in the colony under a natural photoperiod, and mice used in the laboratory tests were maintained and tested under a 14-hour light; 10-hour dark cycle. Mice were drawn at random for testing and were used only once. Food (Wayne Lab-Blox) was scattered *ad libitum* in the enclosures during tests. The water source for mice in the field enclosures was dew and rain, but water bottles with sipper tubes were provided during the laboratory experiment.

All juveniles were maintained under similar conditions in the colony until testing in order to reduce variation in the dependent variables due to differences in early experience (see Russell, 1971). The brood cage population density was the same for all juveniles: the parent pair and four litter mates, usually two males and two females. Culling was done by the time litters were five days old. The bedding

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of brood cages was not changed unless absolutely necessary in order to keep the handling of juveniles to a minimum. Litters were weaned at 21 to 24 days.

Subsequent to weaning, juveniles from a single litter were housed in side-by-side, 130 x 150 x 280 cm cages; males were placed in one side and the females in the other. A section of 6.7-mm-mesh hardware cloth was placed over a tunnel connecting the two sides. Therefore, visual, olfactory, and auditory contacts between the male and female sibs were possible, but copulation was prevented. A section of 1.3-cm-mesh hardware cloth was placed between the water and food sources to insure that all juveniles had experience squeezing through this size opening since they were required to do so during the experiments. Juveniles were 30 to 36 days old at the start of testing.

Breeding pairs provided a constant supply of litters and served as experimental adults. The pairs were maintained in 130 x 150 x 280 cm or 150 x 125 x 280 cm cages and were not separated upon the birth of a litter. Adult males were drawn for the experiments irrespective of the breeding condition of their paired females. Adult females that were to be used in the experiments as nonlactating females were separated from their paired males to prevent pregnancy by using the same type of cage used to separate opposite sex sibs. These females were judged not to be pregnant if they failed to gain weight during a 10-day period immediately prior to being used in the experiments. Lactating females had a one to eight day old litter at the start of an experimental run. All adults were tested with strange juveniles, were in breeding condition at the time of the experiments, and were successful breeders.

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The field and laboratory enclosures differed in respect to size, space complexity, and environmental vicissitudes. The field enclosures were about nine times larger in area than the laboratory enclosures in grassland habitat, and were exposed to the weather. Sixteen 3.8 x 3.8 m enclosures located in grassland habitat were used for the field experiment (Figure 1). Figure 2 gives the spatial arrangement of the field enclosures and describes the surrounding habitat. The walls of the field enclosures were about 66 cm high; the bottom half was 6.7-mm-mesh hardware cloth and the top was aluminum flashing. In order to inhibit burrowing, the hardware cloth was buried and limestone chips were placed by the hardware cloth at the ground surface. Tarpaper was placed over the hardware cloth to prevent mice from seeing other mice in adjacent enclosures and from viewing the surrounding ground-level landscape, but the treeline of a nearby woodlot was possibly within view of the mice. The grass in the enclosures was periodically clipped so that similar habitat was maintained during the course of the study. An electric livestock fence was placed around the periphery of the enclosures to discourage terrestrial predators. Some juveniles disappeared from the field experiments due to unknown reasons. An examination of differences in the tendencies of male and female juveniles to disappear is given in Appendix A.

Twelve 1.2 x 1.2 m masonite enclosures with 0.66 m high walls were used for the laboratory experiment (Figure 1). These enclosures were placed on a tile-covered concrete floor. Figure 3 gives the spatial arrangement of the laboratory enclosures. The "day" period light

Figure 1. The field enclosures (A) and laboratory enclosures (B) used in this study.

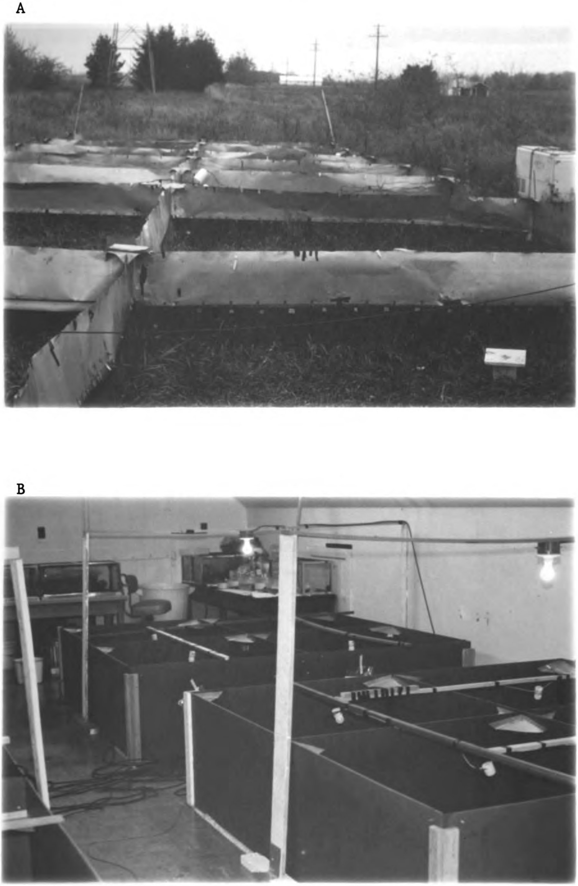


Figure 1.

Figure 2. Arrangement of the field enclosures and description of surrounding habitats. The locations of the resident and dispersal areas (i.e., north-south enclosure pairs) were systematically altered during the experiment to remove habitat selection as a factor in determining the movement of juveniles.

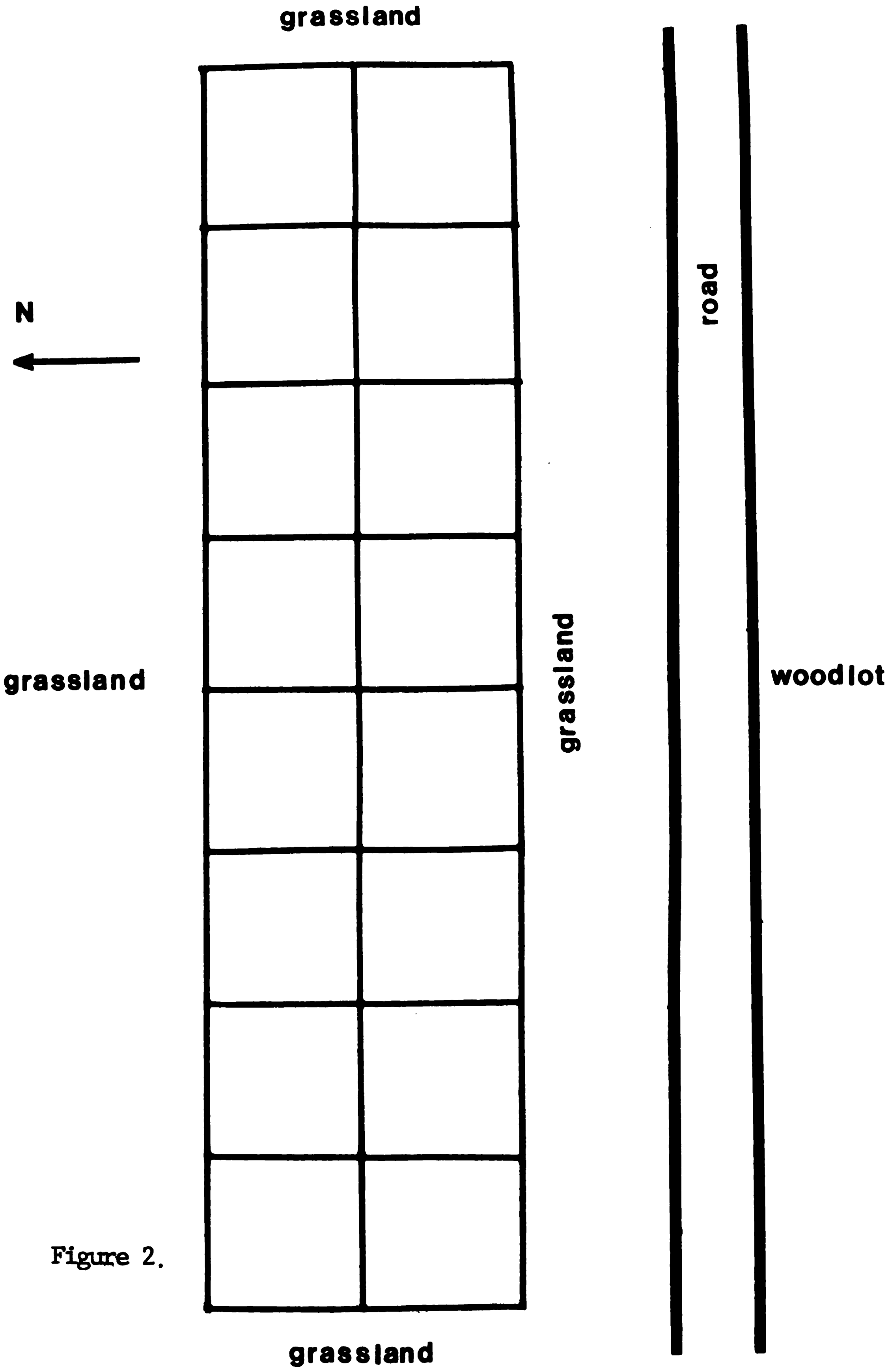
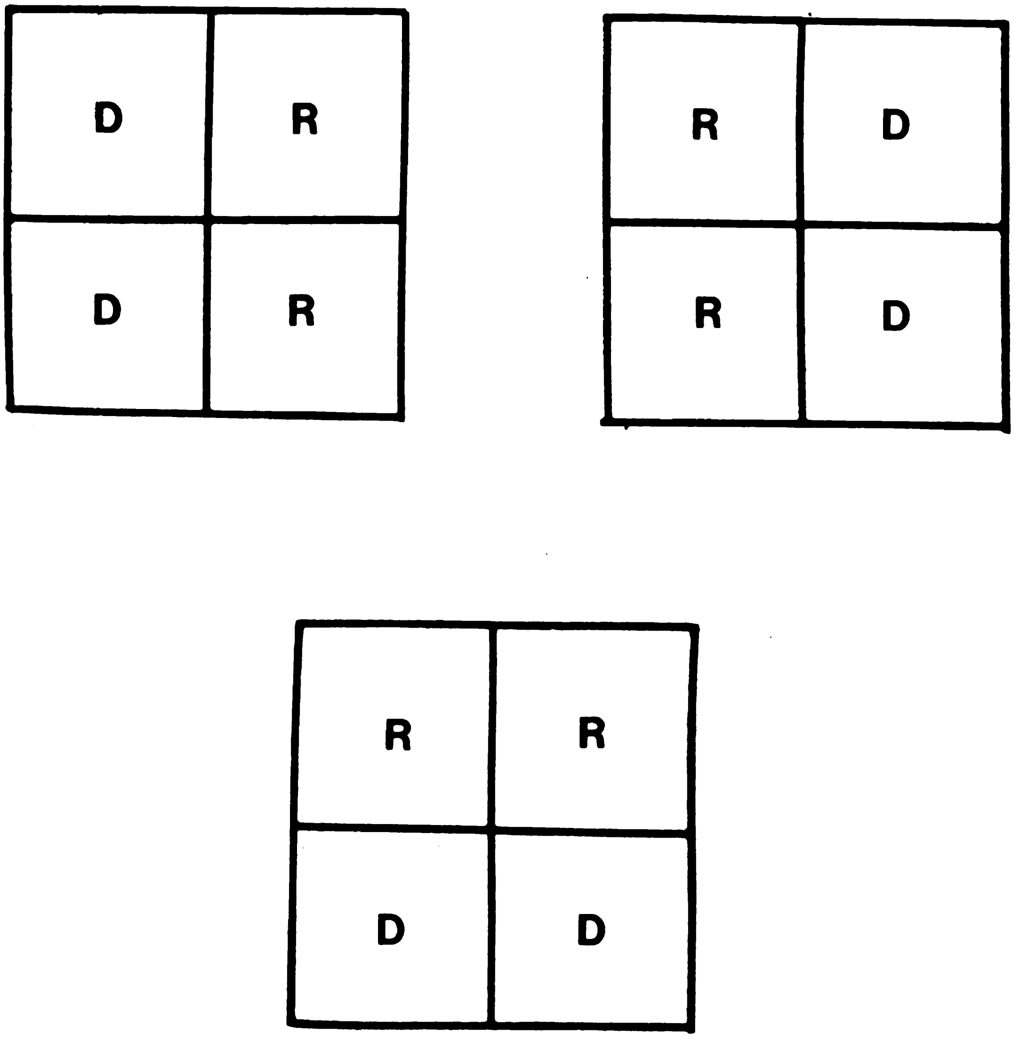


Figure 2.

Figure 3. Arrangement of the laboratory enclosures. The locations of the resident (R) and dispersal (D) areas were the same for all tests.



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D	R

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Figure 3.

intensity was about 3 candlepower white light (a 100-watt bulb over each group of four enclosures) and about 0.25 candlepower red light (a 7.5-watt bulb over each of the enclosures). The "night" period lighting consisted of the red lights alone.

Tunnels

Two-way tunnels (4.3 x 4.8 x 17.5 cm), constructed from 7.8-mm-thick, unpainted Plexiglas, were used to measure the location and activity of juveniles. An operating arm activated a microswitch when a juvenile passed through a tunnel (Figure 4, see A and B, respectively). A section of 6.7-mm-mesh hardware cloth covered with clear plastic sheeting was placed over the tunnel to protect the microswitch from the weather in the field and to discourage mice from activating the operating arm from outside the tunnel (Figure 4, see C). The tunnels were set to be operated by a weight of 7.0 gm; juveniles rarely weighed less than 9.0 gm.

In order to restrict the movement of the adults while allowing the juveniles to move freely through the tunnels, 1.3-cm-mesh hardware cloth rectangular structures hereafter termed restraining grids were placed over the ends of the tunnels (Figure 4, see D). Juveniles could squeeze through the 1.3-cm-square opening in the hardware cloth, but the adults could not (Savidge, 1974). A tunnel, termed the passage tunnel, allowed juveniles to move back and forth between: (1) an enclosure containing an adult or no adult as a control, hereafter termed the resident area and (2) an adjacent enclosure to which the adult did not have access, hereafter termed the dispersal area (Figure 5). The passage tunnels had restraining grids on both ends (Figure 4, see D and D').

Figure 4. The tunnel apparatus used in this study (A = operating arm, B = microswitch, C = tunnel cover, D and D' = restraining grids, and E = feeding station).

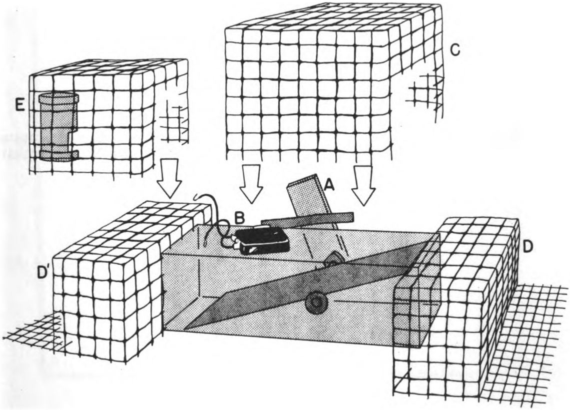

Figure 4.

Figure 5. Example of two experimental enclosure pairs showing the arrangement of passage tunnels (X), feeding stations (F), and nest boxes (O).

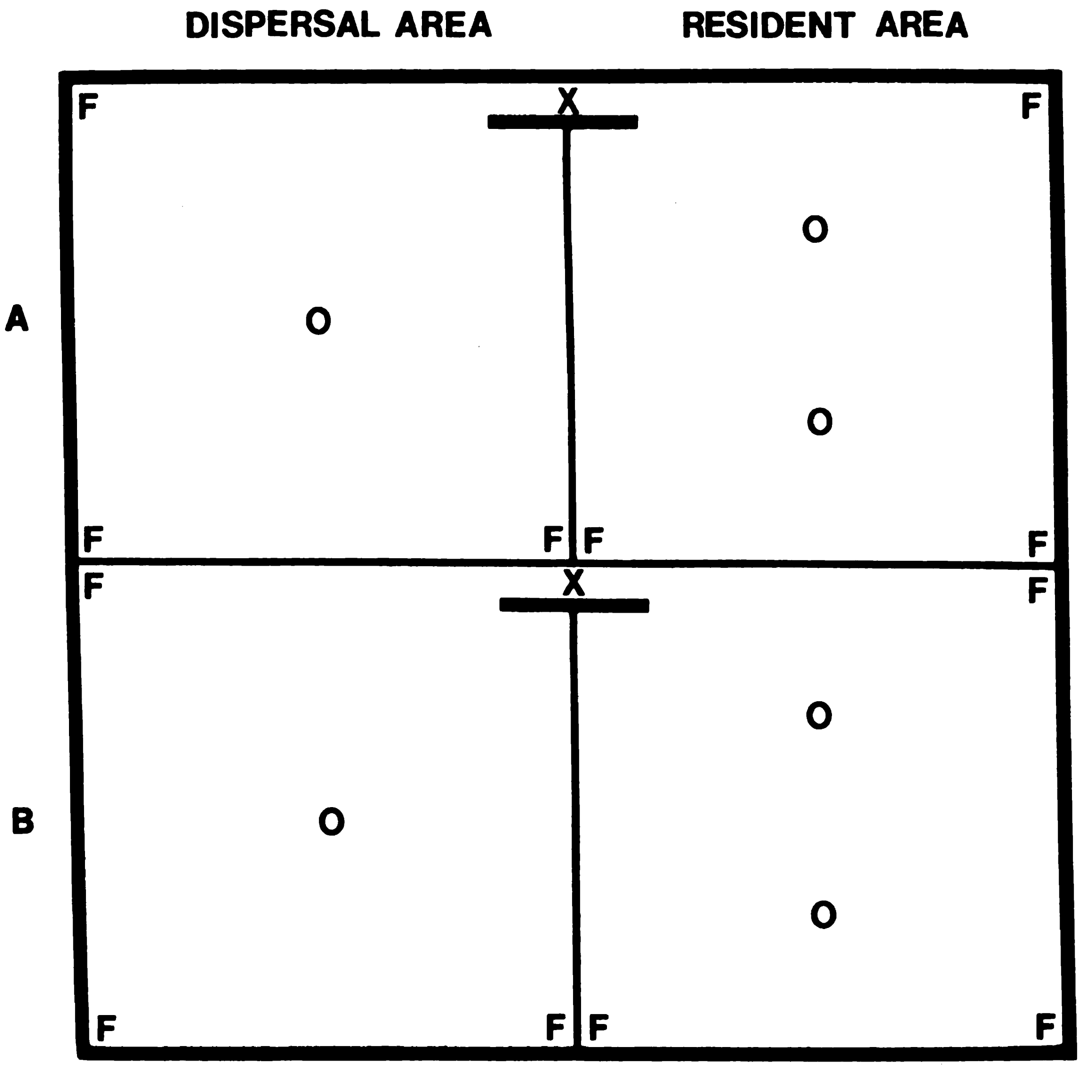

Figure 5.

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Other tunnels were used to measure the activity of juveniles within both the resident and dispersal areas. These tunnels, termed feeder tunnels, had a restraining grid on one end and a feeding station on the other end (Figure 4, see D and E, respectively). The feeding stations were constructed from 6.7-mm-mesh hardware cloth and had a 7.5 dram plastic vial attached to one side. Unhusked sunflower seeds were placed in the vial and could be removed by the juveniles via an opening cut in the bottom of the vial. Feeding stations were placed at random in two of the three available corners of the dispersal and resident areas, respectively. The arrangement of the passage tunnels and feeding stations was the same for the field and laboratory experiments (Figure 5).

Recording Equipment

The microswitches were connected to a 20-channel Esterline-Angus event recorder powered by a 12-volt battery in the field and a 12-volt power supply in the laboratory. The paper speed was 15.24 cm per hour, and the resolution was about 15 sec minimum time between signals.

The activity of juveniles was determined by examining the chart paper. The number of trips made through a passage or feeder tunnel could be counted directly from the paper. The time juveniles spent on either side of the passage tunnel, that is, within the resident area or dispersal areas, could be ascertained by summing the time periods during which the treadle was pointed towards a given area. For example, the microswitch might be off when a juvenile was in the resident area. When the juvenile passed through the tunnel to the dispersal area, the position of the treadle changed and caused the operating arm to turn the microswitch on. Then, the microswitch would be turned off when the juvenile passed back into the resident area again. In this example, the total time the juvenile spent in the resident area could be calculated by summing the two periods during which the microswitch was off.

Nest Boxes

All mice had access to nest boxes during the experiments. Two nest boxes were available in each resident area; one was placed in each dispersal area. The arrangement of the nest boxes was the same for the field and laboratory experiments (Figure 5). Clay drainage tiles were used for nest boxes during the field experiment. These tiles: (1) were of a cylindrical shape, (2) were open at both ends, and (3) were placed vertically in the ground about three-quarters of their length. Circular disks of sheet metal, placed on plastic Petri dishes, were put inside the tiles to serve as the bottoms of the nest boxes. One-half-gallon plastic containers were slipped over the tops of the tiles to prevent sunlight from entering the nest boxes, and 22.6 cm^2 plywood sections were attached to the plastic containers to protect the nest boxes from the weather. A 2.6 cm entry hole was drilled in the side of the tiles. A section of 6.7-mm-mesh hardware cloth, placed on the inside of the tile and extending from the entry hole to the bottom of the nest box, allowed mice to climb in and out. Plastic freezer boxes (1.5 pint) served as nest boxes during the laboratory experiment. These nest boxes were placed on their sides and were taped to the floor. A 1.9 x 2.6 cm access hole was cut in the covers. All nest boxes were supplied with cotton Nestlets (Ancare Corporation) and several lab chow pellets.

Experimental Procedure

An experimental enclosure pair consisted of a resident area and an adjacent dispersal area. Adults were always restricted to resident areas, and juveniles always had access to both resident and dispersal areas. The juveniles and adults were maintained in separate experimental enclosure pairs for a three-night pretest period. For example, a juvenile may have been maintained in enclosure pair A of Figure 5 and an adult may have been maintained in the resident area of enclosure pair B of Figure 5. During the pretest period juveniles could move through passage tunnels to a dispersal area and had access to feeding stations. The restraining grids were placed on the tunnels for the last night of the pretest period. Adults were restricted to a resident area and had access to nest boxes. The present period was intended to allow adults to establish residency in a resident area. Healey (1967) indicated that a two-day period was sufficient for residency establishment. Also, all mice could become accustomed to the experimental environments and the test apparatus (tunnels and/or nest boxes) during pretesting.

The experiments were conducted over four-night periods immediately following the pretesting, and were initiated by placing the juveniles in the resident areas occupied by the adults or containing no adults as controls (*e.g.*, a juvenile might have been removed from enclosure pair A and placed in the resident area of enclosure pair B, Figure 5). The four-day period of time for the experiments was chosen for the following reasons: (1) a longer period in the confined areas may have led to social habituation between the adults and juveniles (Hill, 1970), (2) Healey (1967) noted a dramatic weight change in juveniles after four days exposure to aggressive adults, (3) P. m. bairdi females come into estrus in at least three days upon exposure to males (Bronson and Marsden, 1964), and it was of interest in the present study to determine if juveniles were reproductively competent, and (4) the four-night period allowed a robust measure of consistent differences between the juvenile-adult social combinations.

Procedure Used in the Field Experiment

The sequence of testing the juvenile-adult combinations was randomly chosen to insure that weather conditions in the field did not bias the experiment in a systematic fashion. Juveniles were weighed to the nearest 0.1 gm on a triple beam balance, examined for wounds, and fur-clipped for identification. Adults could be identified by toe-clips made when they were paired for breeding. All mice were placed in plastic cages, driven to the field, and restricted to nest boxes in separate randomly chosen resident areas. These operations were completed by 1000 EST. Nest boxes were opened in the evening prior to the first pretest night by 1900 EST, and all mice could move about in their respective experimental areas during the three-day pretest period. After the three-day pretest period was completed (one juvenile tested in the field experiment as a control was in the pretest condition for four days), juveniles were hand-carried to a resident area containing an adult or no adult as a control and were restricted to an empty nest box by 1000 EST. All tunnels, restraining grids, and feeding stations were removed from the pretest experimental areas, cleaned of urine and feces, and placed in the experimental areas occupied by resident adults or containing no adults. The deer mice were free to interact usually by 1900 EST when the juveniles were released from the nest boxes.

The sleeping sites of the mice were determined each day by quietly looking into nest boxes or searching for surface nests usually before 0900 EST. However, no recordings of activity in the passage and feeder tunnels were examined in detail until the experiments had been completed to avoid introspection of the data. Tunnels were checked for proper functioning every evening by 1900 EST, but some data were lost due to equipment malfunctions.

At the end of the four-night test period all mice were placed in plastic cages and driven to the laboratory usually by 0930 EST. Juveniles were weighed to the nearest 0.1 gm on a triple beam balance and examined for wounds. In order to assure that juveniles were capable of going through the restraining grids, they were usually maintained alone in cages in which the water and food sources were separated by 1.3-cm-mesh hardware cloth for at least one week subsequent to testing. Juvenile females tested with adult males and nonlactating females tested with juvenile males were maintained in individual cages for at least three weeks subsequent to the experiments. These deer mice were checked periodically for the birth of litters to determine if they had been impregnated during the experiments. All other adults were returned to their respective mates. Tunnels, tunnel covers, feeders, restraining grids, and nest boxes were cleaned or replaced at the end of each test. At least one day was skipped between experimental runs to allow degradation of scents deposited by mice in the previous run.

Wecker (1963) showed that _P_. _m_. _bairdi_ selects grassland over woodland habitats. Therefore, since the mice could possibly see the treeline in the woodlot located to the south of the enclosures (Figure 5), the positions of the resident and dispersal areas were reversed for every replication of juvenile-adult combinations. For example, one experimental run using a juvenile male and an adult male might have had the resident area to the south, and the next replicate of the juvenile male-adult male social combination would have had the resident area to the north. This removed habitat selection (i.e., moving away from the woodlot) as a possible consistent influence on the movement of juveniles between the resident and dispersal areas. Field testing was conducted during June to October, 1975.

Procedure Used in the Laboratory Experiment

Treatment of mice used in the laboratory and field tests was the same, except that the animals were hand carried in plastic cages to the laboratory. Also, since behavioral observations were made in the laboratory, juveniles were randomly chosen by another individual to insure that the sex of juveniles was unknown to the observer. Mice were placed in separate resident areas and restricted to nest boxes by 1315 EST. All mice were released from the nest boxes between 1850 and 1900 EST immediately prior to the 10-hour "night" period (1900 to 0500 EST).

The sleeping sites of the mice were observed by 1200 EST, and the correct operation of equipment was usually verified between 1700 and 1830 EST. Laboratory pretest and test procedures were the same as in the field experiment, except that juveniles in one replication within each of three treatment combinations had two days experience with the restraining grids instead of only one day. Mice were returned to the colony by 0930 EST following the last test night. All equipment, including the pens, was thoroughly cleaned and another experimental run was started the same day by 1315 EST.

Mice were observed from a platform or stepladder overlooking the resident area on the first and last night of the test periods. The observations usually started about 10 to 15 minutes into the "night" period. Each resident area was observed for a 15-second interval every minute for 60 consecutive minutes. Observations were continuous in most cases because coded behaviors were noted by speaking softly into a tape recorder while the attention of the observer remained on the mice. The tapes were transcribed at a later time. During one night the codes were simply written on paper, and the observer had to briefly look away from the mice. The following definitions of behaviors reported upon in this paper were used:

(1) <u>Chasing</u> -- one mouse rushing at another and the latter running away

(2) <u>Fight</u> -- locked fight

(3) <u>Avoidance</u> -- a mouse moving away as another approached without rushing

(4) <u>Mutual avoidance</u> -- both mice moving away after one approached

The avoidance behavior was noted only when mice were no more than 30 to 45 cm apart at the time one or both moved. A behavior was scored more than once in a single 15-second interval if a mouse stopped the behavior, engaged in a different behavior, and then initiated the former behavior. The lab testing was conducted during January to April, 1976.

Dependent Variables

The basic objective of this research was to obtain quantitative measures of the outcome of social interactions between juvenile and adult prairie deer mice. In order to achieve this objective, several dependent variables were measured. The variables represented three different categories: (1) juvenile settlement, (2) juvenile weight change, and (3) descriptive variables.

Juvenile Settlement

The effects of social factors on the settlement of juveniles were evaluated experimentally by measuring three aspects of the spatial relationships of juveniles and adults within the enclosures. If the social factors examined in this study affect the settlement of juveniles, then there should be differences in the propensity of juveniles to (1) nest, during the daytime inactive period, in enclosures occupied by adults, (2) share a nest with adults if juveniles nest in enclosures occupied by adults, and/or (3) remain in enclosures occupied by adults during the night-time active period.

Nesting Area. The area in which juveniles nested during daytime was observed on 315 out of the 320 days of the experiments. On five days juveniles could not be found during the field experiment, and the position of the passage tunnel treadle was used to indicate their location. In a few cases during both the field and laboratory experiments, juveniles were located in the passage tunnel and were scored as being in the dispersal area since they had moved from the resident area.

Nesting Arrangement. The nesting arrangement of adults and those juveniles that remained in the resident area was determined. The arrangement was scored as mutual nesting or nesting separately. In all cases, except one when the mice shared a surface nest, juveniles and adults that nested together did so in nest boxes.

Amount of Time in the Resident Area. An estimate of time that juveniles spent in the resident area, expressed as the per cent of the total active period, was made from the recordings of activity in the passage tunnel. This measure must be considered an estimate because juveniles could go through the passage tunnel, but still could remain in the restraining grid rather than truly enter the resident area. Therefore, activity in the passage tunnel did not necessarily measure the time juveniles were freely moving in the resident area.

The active period during field tests was taken as the period from sunset to sunrise as reported by the U. S. National Weather Service for East Lansing, Michigan. The active period during laboratory testing was considered to be the 10-hour "night" period. There was some juvenile activity during the day periods, but this was ignored in the analysis. Some data were lost due to equipment malfunction when electrical connections became loose or tunnels were tripped in the wrong direction. In these cases, the active period was taken in the total time during the night period when the tunnel was operating correctly.

I chose to take these measures because each provided an estimate of the mutual use of the resident area by juveniles and adults, and the incorporation of three measures allowed greater precision in establishing the juvenile-adult spatial relationships compared to the home range overlap measures commonly taken in field studies (e.g., Metzgar, 1971). A significant difference in one or more of the settlement measures among social combinations chosen for the present study was interpreted as indicating a relative limitation of juvenile settlement.

The measures of juvenile settlement could be expressed either as daily and nightly values or total and mean scores. Table 2 gives a summary of the outcomes possible for all three variables.

Table 2. The outcomes possible for the three measures of settlement used in this study.

	Nesting Area of Juveniles	Nesting Arrangement for Juveniles that Nested in the Resident Area	Per Cent Time Juveniles Spent in the Resident Area
Outcome	Resident area or Dispersal area	With Adult or Alone	100% to 0%

Juvenile Weight Change

The weight change of juveniles was measured by determining the difference between their initial and final weights. This dependent variable was chosen because the effects of social factors on the maturation of juvenile small rodents has not been critically examined under experimental conditions, such as those of the present study, that allowed juveniles to avoid interactions with adults and that maintained all juveniles for measurement.

Descriptive Variables

In order to further quantify the effects of the social factors and to gain insight into the behaviors and social relationships involved in interactions between juveniles and adults, several descriptive measures were taken. These measures were related to juvenile activity, wounding of juveniles, direct observation of social interactions during the laboratory experiment, and reproduction.

Juvenile Activity. Two aspects of juvenile activity were measured: (1) activity between the resident and dispersal areas and (2) activity within the resident and dispersal areas. The activity in the passage tunnel provided a measure of the frequency of juvenile movements between the resident and dispersal areas. These data were expressed as the number of tunnel trips per hour of the active period. Analysis of the passage tunnel activity indicated whether the rate of movement between areas was influenced by social factors.

The activity in the feeder tunnels provided an estimate of the frequency of juvenile movements within the resident and dispersal areas. These data were expressed as the number of tunnel trips per hour during which feeders were available to the juveniles. For example, if a juvenile was in the resident area for three hours during the active period, total number of feeder hours was six since there were two feeders available in the area. This measure must be considered a gross estimate of activity because of interfering variables. Differences in movement could have been due to differences in individual preferences for sunflower seeds or in propensities of juveniles to escape adults by seeking refuge in the feeding stations. These data will be presented in Appendix B.

Wounding. The wounding of juveniles by adults was determined by making a direct count. Care was taken to avoid double counts (i.e., wounds inflicted by upper and lower incisors). Therefore, a wound was considered to be the result of one bite.

Direct Observations. Behavioral interactions between juvenile-adult social combinations were observed.

Reproduction. The number of adult and juvenile females that became pregnant during the experiments was determined.

Statistical Procedures

The dependent variables chosen for evaluation provided data that were discrete and analyzed with chi square tests or continuous and analyzed with nonparametric or parametric procedures. The four-day total and daily nesting area frequencies were analyzed with multi-way chi square tests (Gill, 1976), but only the four-day total analyses are presented in the results section. The results of tests on the daily values are given in Appendix C. The data were treated in this manner because for all comparisons except one, the total and daily analyses had the same outcomes for at least three of the four days. Also, the chi square approximation may be poor for the daily tests because of the small expected frequencies in some cells.

The four-day total frequencies represent an artificial four-fold increase in sample size since the same juveniles were scored over the four-night periods. Ferguson (1966) pointed out that as sample size and differences between samples increases by a constant multiplicative factor, the χ^2-value will also increase by the same constant factor. Therefore, since many juveniles remained in the same area on all four days (64 of 80 tested), the calculated χ^2-values for the four-night total frequencies were divided by four to arrive at a very conservative adjusted critical value taking the lack of statistical independence into account.

The four-day total nesting arrangement frequencies were analyzed with multi-way chi square tests, but the daily values were not analyzed due to the extremely low expected frequencies in many cells. The calculated χ^2-values were divided by four to adjust for the lack of statistical independence across days because 27 out of the 37 juveniles that remained in the resident area on all four days did not change nesting arrangements.

It should be pointed out that the degrees of freedom for the multi-way chi square tests are based on the number of criteria of classification rather than the number of rows and columns (Gill, 1976). For example, prior to testing for differences in the individual main effects of location, juvenile sex, and adult class (i.e., pooling data for other main effects), it was necessary to determine if differences in the proportions of juveniles that nested in the resident area and/or nested with adults existed among the 16 treatment groups (i.e., 2 locations x 2 juvenile classes x 4 adult classes) by using a 16 x 2 contingency table. In these tests, df = (2-1)(2-1)(4-1)(2-1) = 3 since there were 2 locations, 2 juvenile classes, 4 adult classes, and 2 areas or 2 possible nesting arrangements.

Two-way contingency tables were used for some comparisons of nesting area, nesting arrangement, and tunnel utilization data. Yates' correction for continuity was not used as suggested by Conover (1974).

The four-night means of the per cent time measure and both the passage and the feeder tunnel activity rate measures in the field experiment were examined by nonparametric Kruskal-Wallis and Wilcoxin's rank-sum tests. Parametric procedures could not be used because the raw data could not be transformed to meet the required assumptions. However, the nonparametric procedures used in this study allowed the same comparisons as those possible in a 2 x 4 factorial analysis of variance. The field experiment had one missing replication due to

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equipment malfunction. The missing datum was replaced with the group mean rather than replacing all replication scores with the group mean as suggested by Bradley (1968). This procedure was followed because the large number of ties would have magnified the existing differences.

Four-night means and nightly scores were used for comparisons of the per cent time and passage tunnel activity rate measures in the laboratory experiment. The raw data for each replication were transformed to the arcsin and $\sqrt{y + 1/2}$ scales, respectively. However, only the four-night mean scores were used for comparisons of the feeder tunnel activity rates. The raw data for each of these replication means were transformed to the $\sqrt{y + 1/2}$ scale. Each dependent variable above was analyzed by a 2 x 4 factorial analysis of variance.

Comparisons of the changes in juvenile weights in the field and laboratory experiments were analyzed by a 2 x 2 x 4 (i.e., location x juvenile sex x adult class) factorial analysis of variance. Transformation was not required for the weight change data.

Homogeneity of variances was confirmed using the F-max test. Differences among some simple main effect means were examined by *a posteriori* Student-Newman-Keuls tests. The parametric methods were described by Sokal and Rohlf (1968) and Winer (1971). The nonparametric procedures followed Bradley (1968) and Sokal and Rohlf (1968). *A priori* significance levels were set at alpha = .05 for all statistical tests. Two tailed tests were used throughout. The analyses of variance and chi square tests were done on the Wang 600-14 calculator in the Michigan State University Museum.

RESULTS

The results of the experiments have been organized into three subsections under the headings of juvenile settlement, juvenile weight change, and descriptive measures. The first subsection contains the analyses of the settlement measures and juvenile activity in the passage tunnel. The effects of the experimental treatments on the weight changes of juveniles are evaluated in the second subsection. The wounding, behavioral observation, and reproduction data are presented in the final subsection.

Juvenile Settlement

Nesting Area. The propensity of juveniles to nest within field or laboratory enclosures occupied by an adult was examined to determine the effects of the social factors on juvenile settlement. Prior to testing for differences in individual main effects by pooling data for the remaining main effects, it was necessary to determine if differences existed among the 16 treatment groups by using a 16 x 2 contingency table. The percentages for this comparison are given in Table 3. The four-day total proportion of juveniles that nested within the resident area was not jointly independent of location of the experiment, juvenile sex, and adult class ($\chi^2_{adj} = 28.3820$, df = 3, $.005 > P$). Therefore, the data could not be pooled to test for any single main effect. The four-day total nesting area frequencies obtained in the

Table 3. Summary of the daily and four-day total group mean percentages of the juveniles that nested in the resident area.

Table 3. Summary of the daily and four-day total group mean percentages of the juveniles that nested in the resident area.

	Field Experiment							
	Juvenile Male				Juvenile Female			
	Adult Male	Nonlactating Female	Lactating Female	Control (No Adult)	Adult Male	Nonlactating Female	Lactating Female	Control (No Adult)
Day 1	100[a]	100	80	80	100	80	80	100
Day 2	100	80	80	80	80	60	75*	100
Day 3	100	100	80	80	100	60	60	100
Day 4	100	80	80	80	80	60	60	100
Four-day total	100	90	80	80	90	65	68	100

	Laboratory Experiment							
	Juvenile Male				Juvenile Female			
	Adult Male	Nonlactating Female	Lactating Female	Control (No Adult)	Adult Male	Nonlactating Female	Lactating Female	Control (No Adult)
Day 1	100	100	20	80	80	40	40	40
Day 2	100	100	0	100	80	40	20	60
Day 3	100	100	0	60	60	40	20	60
Day 4	100	80	20	60	60	40	20	0
Four-day total	100	95	10	75	70	40	25	40

a = each column represents 5 juveniles tested over a four-day period.

*N = 4 for one day when a juvenile was inadvertently restricted to a nest box.

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field and laboratory experiments were analyzed separately to determine the effects of the social factors on juvenile settlement.

In the field experiment, the proportion of juveniles that nested within the resident area was jointly independent of juvenile and adult social conditions (8 x 2 contingency table, Table 4). These data could be pooled to test for differences between male and female juveniles and among adult classes. A 2-way contingency analysis showed that there was no significant difference in the proportions of juvenile males and juvenile females that nested within the resident area (Table 5). Differences among adult classes for data pooled from the juvenile sexes were also nonsignificant (Table 6). In conclusion, under field enclosure conditions, the use of nesting areas by juveniles was not dependent upon the sex of juveniles or the sex of adults/reproductive stage of adult females.

In the laboratory experiment, the proportion of juveniles that nested within the resident area was not jointly independent of juvenile and adult social factors (8 x 2 contingency table, $.005 > P$, Table 7). It was necessary to test for differences between juvenile males and females separately for each adult class (2-way contingency tables) and to test for differences among adult classes separately for juvenile males and females (4 x 2 contingency tables).

There were no significant differences in the proportions of juvenile males and juvenile females that nested within the resident area for adult males (Table 8); for nonlactating females ($P \approx .065$, Table 9); for lactating females (Table 10); and for controls with no adults (Table 11). However, there was a significant difference among adults for juvenile males ($.01 > P > .005$, Table 12). Inspection of Table 12

Table 4. Chi square analysis of the four-day total nesting area frequencies of juveniles for the eight treatment combinations used in the field experiment.

	Juvenile Male		Juvenile Female	
Area:	Resident	Dispersal	Resident	Dispersal
<u>Adult</u>				
Male	20	0	18	2
Nonlactating Female	18	2	13	7
Lactating Female	16	4	13*	6*
Control (No Adult)	16	4	20	0

χ^2_{adj} = 4.5542, df = 3, .5 > P > .1; N = 19*

Table 5. Chi square analysis of the four-day total nesting area frequencies of male and female juveniles during the field experiment. The data were pooled for the adult classes.

	Resident Area	Dispersal Area
Juvenile Male	70	10
Juvenile Female	64*	15*

χ^2_{adj} = 0.3156, df = 1, .9 > P > .5; N = 79*

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Table 6. Chi square analysis of the four-day total nesting area frequencies of juveniles during the field experiment. The data were pooled for the juvenile sexes to examine differences among the adult classes.

Area:	Resident	Dispersal
<u>Adult</u>		
Male	38	2
Nonlactating Female	31	9
Lactating Female	29*	10*
Control (No Adult)	36	4

$\chi^2_{adj} = 2.1853$, df = 3, $.9 > P > .5$; N = 39*

Table 7. Chi square analysis of the four-day total nesting area frequencies of juveniles for the eight treatment combinations used in the laboratory experiment.

	Juvenile Male		Juvenile Female	
Area:	Resident	Dispersal	Resident	Dispersal
<u>Adult</u>				
Male	20	0	14	6
Nonlactating Female	19	1	8	12
Lactating Female	2	18	5	15
Control (No Adult)	15	5	8	12

$\chi^2_{adj} = 15.4865$, df = 3, $.005 > P$

Table 8. Chi square analysis of the four-day total nesting area frequencies of juvenile males and females for adult males during the laboratory experiment.

Area:	Resident	Dispersal
Juvenile Male	20	0
Juvenile Female	14	6

$\chi^2_{adj} = 1.7645$, df = 1, $.5 > P > .1$

Table 9. Chi square analysis of the four-day total nesting area frequencies of juvenile males and females for nonlactating females during the laboratory experiment.

Area:	Resident	Dispersal
Juvenile Male	19	1
Juvenile Female	8	12

$\chi^2_{adj} = 3.4473$, df = 1, $P \approx .065$

Table 10. Chi square analysis of the four-day total nesting area frequencies of juvenile males and females for lactating females during the laboratory experiment.

Area:	Resident	Dispersal
Juvenile Male	2	18
Juvenile Female	5	15

$\chi^2_{adj} = 0.3896$, df = 1, $.9 > P > .5$

Table 11. Chi square analysis of the four-day total nesting area frequencies of juvenile males and females for the control with no adult during the laboratory experiment.

Area:	Resident	Dispersal
Juvenile Male	15	5
Juvenile Female	8	12

$\chi^2_{adj} = 1.2532$, df = 1, $.5 > P > .1$

Table 12. Chi square analysis of the four-day total nesting area frequencies of juvenile males during the laboratory experiment.

Area:	Resident	Dispersal
<u>Adult</u>		
Male	20	0
Nonlactating Female	19	1
Lactating Female	2	18
Control (No Adult)	15	5

$\chi^2_{adj} = 12.2619$, df = 3, $.01 > P > .005$

Table 13. Chi square analysis of the four-day total nesting area frequencies of juvenile females during the laboratory experiment.

Area:	Resident	Dispersal
<u>Adult</u>		
Male	14	6
Nonlactating Female	8	12
Lactating Female	5	15
Control (No Adult)	8	12

$\chi^2_{adj} = 2.1714$, df = 3, $.9 > P > .5$

reveals that juvenile males nested in the resident area less frequently when lactating females, compared to adult males, nonlactating females, and the control condition with no adult, were encountered. The proportion of juvenile females that nested within the resident area was similar for all adult classes (Table 13).

These results show that under laboratory conditions, the use of nesting areas by juveniles was not dependent upon their sex. However, juvenile males tended to nest in resident areas occupied by nonlactating females more frequently than did juvenile females at a borderline significance level of alpha ≃ .065. The use of nesting areas by juveniles was significantly dependent upon the sex of adults/reproductive stage of adult females for juvenile males, but not juvenile females. Lactating females, compared to the other adult classes, repulsed juvenile males. Figure 6 gives a summary of the four-day total frequencies of juvenile nesting areas.

<u>Nesting Arrangement</u>. The propensity of juveniles to nest with adults was examined to determine the effects of the social treatments on a second aspect of juvenile settlement under two environmental conditions. Days on which juveniles nested in the dispersal areas were not included in this analysis since it was of interest to examine whether differences in nesting arrangement due to social factors existed when juveniles nested in areas occupied by adults. Inclusion of juveniles irrespective of their nesting area would have distorted the findings. Also, the control juveniles were omitted from this analysis.

As was the case for the nesting area measure, the four-day total proportion of juveniles that nested with adults was not jointly independent of location of the experiment, juvenile sex, and adult class

Figure 6. Four-day total nesting area frequencies of juveniles (N = 20 juvenile days). The designations for adults (♂ = male, ♀ = nonlactating female, LAC ♀ = lactating female, and CON = control with no adult) will be used for other figures in this paper.

● = JUVENILE MALE
△ = JUVENILE FEMALE
:: B. LAB EXPERIMENT

A. FIELD EXPERIMENT

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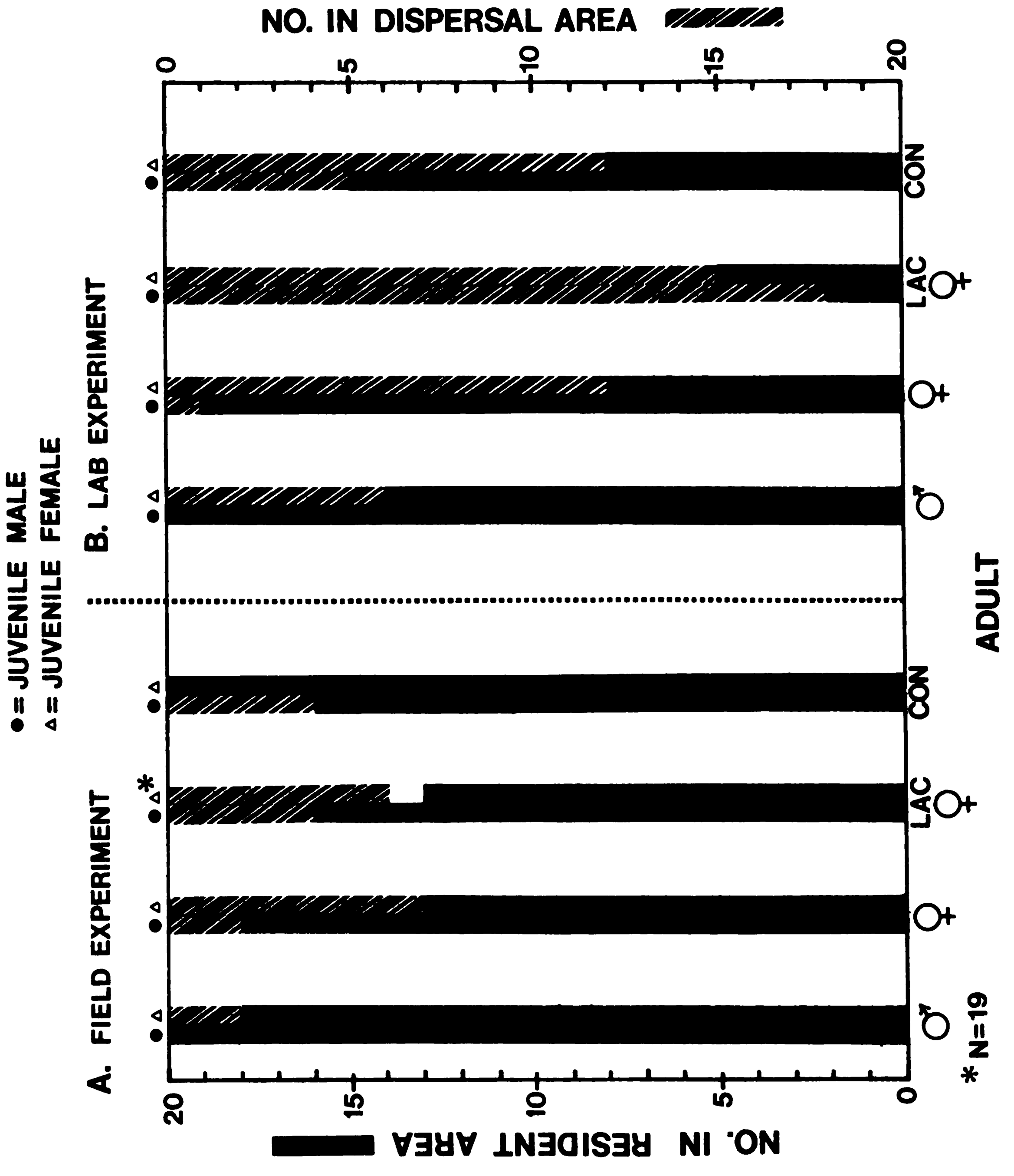
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Figure 6.

(χ^2_{adj} = 19.0299, df = 2, .005 > P). The percentages for this comparison are given in Table 14. The effects of the social factors on nesting arrangement were examined by conducting separate analyses of the four-day total frequencies obtained in the field and laboratory experiments.

In the field experiment, the proportion of juveniles that nested with adults was not jointly independent of juvenile and adult social conditions (6 x 2 contingency table, .01 > P > .005, see Table 14 for the raw data). It was necessary to test for differences between juvenile males and juvenile females separately for each adult class (2-way contingency tables) and to test for differences among adult classes separately for juvenile males and juvenile females (3 x 2 contingency tables).

There were no significant differences in the proportions of juvenile males and juvenile females that nested with adult males (Table 15), but juvenile males nested with nonlactating females more frequently than did juvenile females (.025 > P > .01, Table 16). The proportions of the juvenile sexes that nested with lactating females were similar (Table 17); one juvenile male nested for three days with a lactating female that had abandoned her litter. Differences among adult classes were nonsignificant for juvenile males (Table 18) and juvenile females (Table 19). But juvenile females tended to nest more frequently with adult males than with either nonlactating females or lactating females at a borderline significance of alpha ≈ .07 (Table 19).

These results show that, under field enclosure conditions, the nesting arrangement of juveniles was significantly dependent upon the sex of the juveniles, but only when nonlactating females are encountered. Juvenile males nested with nonlactating females more frequently

Table 14. Summary of the daily and four-day total group mean percentages of the juveniles that nested with adults.

Table 14. Summary of the daily and four-day total group mean percentages of the juveniles that nested with adults.

	Field Experiment					
	Juvenile Male			Juvenile Female		
	Adult Male	Nonlactating Female	Lactating Female	Adult Male	Nonlactating Female	Lactating Female
Day 1	80 (5)^a	80 (5)	0 (4)	60 (5)	0 (4)	0 (4)
Day 2	60 (5)	50 (4)	25 (4)	50 (4)	0 (3)	0 (3)
Day 3	60 (5)	100 (5)	25 (4)	80 (5)	0 (3)	0 (3)
Day 4	60 (5)	100 (4)	25 (4)	50 (4)	0 (3)	0 (3)
Four-day total	65 (20)^b	83 (18)	19 (16)	61 (18)	0 (13)	0 (13)

	Juvenile Male			Juvenile Female		
	Adult Male	Nonlactating Female	Lactating Female	Adult Male	Nonlactating Female	Lactating Female
Day 1	60 (5)	60 (5)	0 (1)	75 (4)	100 (2)	0 (2)
Day 2	60 (5)	100 (5)	0 (0)	75 (4)	100 (2)	0 (1)
Day 3	80 (5)	80 (5)	0 (0)	100 (3)	100 (2)	0 (1)
Day 4	80 (5)	100 (4)	0 (1)	100 (3)	100 (2)	0 (1)
Four-day total	70 (20)	84 (19)	0 (2)	86 (14)	100 (8)	0 (5)

a = number of juveniles that remained in the resident area and were free to nest with the adult.
b = four-day total of juvenile days in the resident area.
Note: Only days on which juveniles nested in the resident area are included.

Table 15. Chi square analysis of the four-day total nesting arrangement frequencies of male and female juveniles for adult males during the field experiment.

	Nested With Adult	Did Not Nest With Adult
Juvenile Male	13	7
Juvenile Female	11	7

$\chi^2_{adj} = 0.0154$, df = 1, $.9 > P > .5$

Note: Only days on which juveniles nested in the resident area are included.

Table 16. Chi square analysis of the four-day total nesting arrangement frequencies of male and female juveniles for nonlactating females during the field experiment.

	Nested With Adult	Did Not Nest With Adult
Juvenile Male	15	3
Juvenile Female	0	13

$\chi^2_{adj} = 5.2474$, df = 1, $.025 > P > .01$

Note: Only days on which juveniles nested in the resident area are included.

Table 17. Chi square analysis of the four-day total nesting arrangement frequencies of male and female juveniles for lactating females during the field experiment.

	Nested With Adult	Did Not Nest With Adult
Juvenile Male	3	13
Juvenile Female	0	13

$\chi^2_{adj} = 0.6796$, df = 1, $.5 > P > .1$

Note: Only days on which juveniles nested in the resident area are included.

Table 18. Chi square analysis of the four-day total nesting arrangement frequencies of juvenile males for adults during the field experiment.

	Nested With Adult	Did Not Nest With Adult
Adult Male	13	7
Nonlactating Female	15	3
Lactating Female	3	13

$\chi^2_{adj} = 3.7996$, df = 2, $.5 > P > .1$

Note: Only days on which juveniles nested in the resident area are included.

Table 19. Chi square analysis of the four-day total nesting arrangement frequencies of juvenile females for adults during the field experiment.

	Nested With Adult	Did Not Nest With Adult
Adult Male	11	7
Nonlactating Female	0	13
Lactating Female	0	13

$\chi^2_{adj} = 5.2963$, df = 2, $P \approx .07$

Note: Only days on which juveniles nested in the resident area are included.

Table 20. Chi square analysis of the four-day total nesting arrangement frequencies of male and female juveniles for adult males during the laboratory experiment.

	Nested With Adult	Did Not Nest With Adult
Juvenile Male	14	6
Juvenile Female	12	2

$\chi^2_{adj} = 0.2826$, df = 1, $.9 > P > .5$

Note: Only days on which juveniles nested in the resident area are included.

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than did juvenile females. The four-day total proportions of juvenile males and females that nested with adult males or lactating females were similar; juveniles tended to nest with adult males, but tended not to nest with lactating females. There was some evidence to indicate that the nesting arrangement is dependent upon the adult class. The four-day total proportions of juvenile males that nested with adult males or nonlactating females were much higher, though not significant, than the four-day total proportion of juvenile males that nested with lactating females. Juvenile females never nested with nonlactating females or lactating females, but frequently nested with adult males. This difference in four-day total proportions closely approached significance ($P \approx .07$).

In the laboratory experiment, the proportion of juveniles that nested with adults was again not jointly independent of juvenile and adult social conditions (6 x 2 contingency table, $.05 > P > .025$, see Table 14 for the raw data). No significant differences were found between the proportions of juvenile males and juvenile females that nested with the adults when compared separately for adult males (Table 20) and nonlactating females (Table 21). A chi square test for lactating females was judged not to be meaningful; the expected frequencies were extremely small since juveniles seldom nested in areas occupied by adults. On neither of the two days that juvenile males nested within enclosures containing lactating females nor on none of the five days that juvenile females nested within enclosures containing lactating females did the juveniles nest with the adults. Differences among adult males, nonlactating females, and lactating females when compared

Table 21. Chi square analysis of the four-day total nesting arrangement frequencies of male and female juveniles for nonlactating females during the laboratory experiment.

	Nested With Adult	Did Not Nest With Adult
Juvenile Male	16	3
Juvenile Female	8	0

$\chi^2_{adj} = 0.3553$, df = 1, $.9 > P > .5$

Note: Only days on which juveniles nested in the resident area are included.

Table 22. Chi square analysis of the four-day total nesting arrangement of juvenile males for adults during the laboratory experiment.

	Nested With Adult	Did Not Nest With Adult
Adult Male	14	6
Nonlactating Female	16	3
Lactating Female	0	2

$\chi^2 = 1.6841$, df = 2, $.5 > P > .1$

Note: Only days on which juveniles nested in the resident area are included.

separately for juvenile males (Table 22) and juvenile females (Table 23) were nonsignificant.

These findings are in conflict with the results of the chi square test for overall 3-way independence. Inspection of Table 14 indicates that juveniles nested with adult males and nonlactating females more frequently than with lactating females. However, a 3 x 2 contingency table using pooled data showed that significance was only borderline at alpha ≈ .06 (Table 24). This probability statement must be viewed with caution because the test was suggested upon inspection of the data. The failure to detect significant differences in the pooled data may be due to the small number of juveniles that remained in the resident area for some treatment groups, which may have been compounded by the overly conservative adjusted total chi square value. The four-day total nesting arrangement frequencies are given in Figure 7.

These results show that, in the laboratory experiment, the nesting arrangement of juveniles and adults was not dependent upon the sex of juveniles. Both juvenile males and females tended to nest with adult males or nonlactating females, but juveniles never nested with lactating females. This difference in the adult classes was very close to being significant.

Time in the Resident Area. The amount of time, expressed as the per cent of the active period, juveniles spent in the resident areas of the field and laboratory enclosures was examined to determine the effects of the social factors on a third aspect of juvenile settlement. Significantly more juveniles remained in the resident areas during the active period in the field experiment compared to the laboratory

Table 23. Chi square analysis of the four-day total nesting arrangement frequencies of juvenile females for adults during the laboratory experiment.

	Nested With Adult	Did Not Nest With Adult
Adult Male	12	2
Nonlactating Female	8	0
Lactating Female	0	5

$\chi^2_{adj} = 4.5184$, df = 2, $.5 > P > .1$

Note: Only days on which juveniles nested in the resident area are included.

Table 24. Chi square analysis of the four-day total nesting arrangement frequencies of pooled juvenile males and females for adults during the laboratory experiment.

	Nested With Adult	Did Not Nest With Adult
Adult Male	26	8
Nonlactating Female	24	3
Lactating Female	0	7

$\chi^2_{adj} = 5.7170$, df = 2, $P \simeq .06$

Note: Only days on which juveniles nested in the resident area are included.

Figure 7. Four-day total nesting arrangement frequencies. Only days on which juveniles nested in the resident areas are shown.

● = JUVENILE MALE

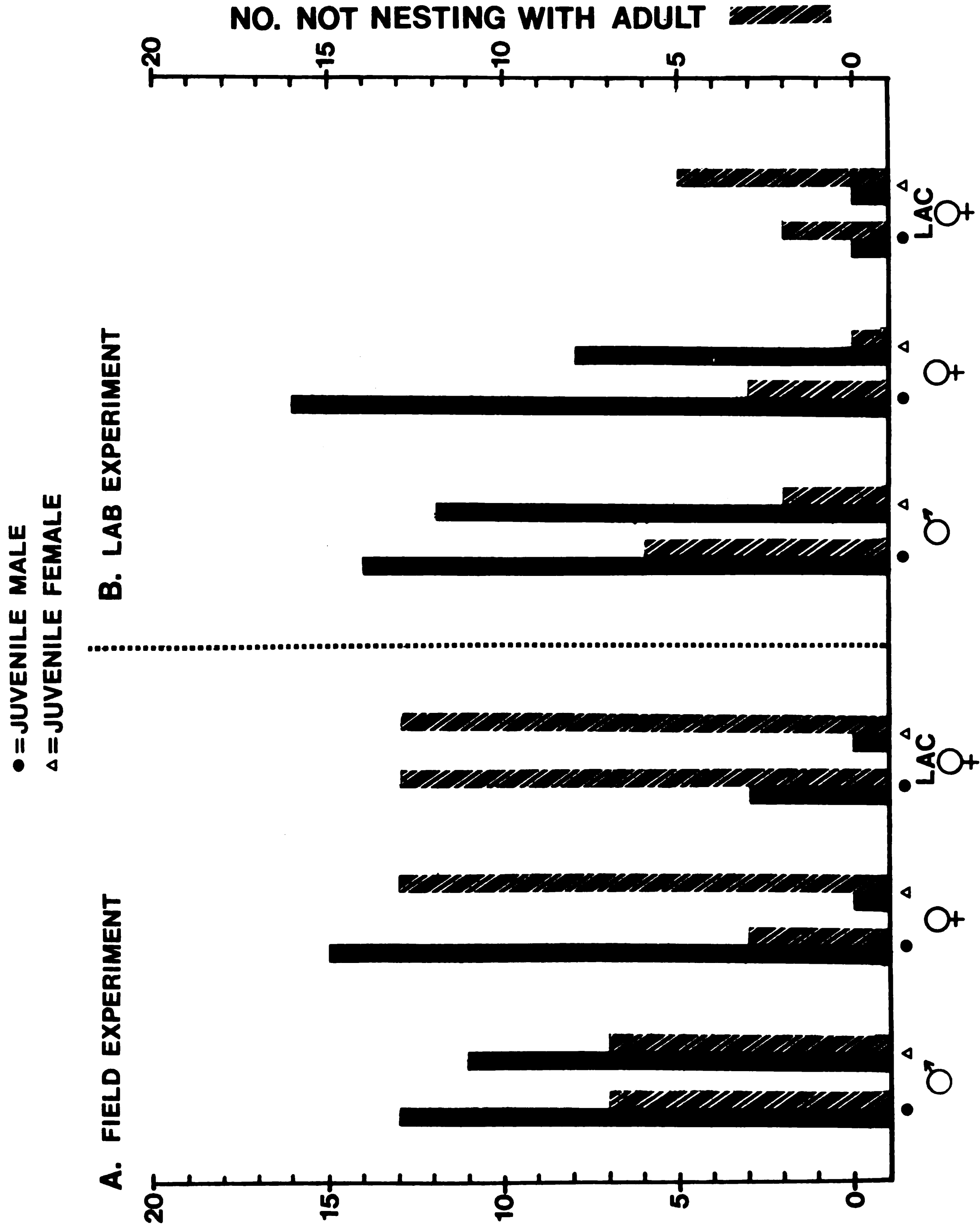
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Figure 7.

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experiment (.005 > P, Table 25). This probability statment must be viewed with caution because the test was suggested upon examination of the data. The significant difference above can be attributed to the environmental treatments for two reasons. Firstly, all but one of the juveniles in the field experiment used the apparatus (passage and feeder tunnels) during the pretest period prior to the placement of the restraining grids (Table 26). Secondly, all juveniles were required to go through the holes in a section of 1.3-cm-mesh hardware cloth prior to the experiments and usually for at least one week following the experiments in order to secure food and water. Therefore, it was assured that all juveniles were capable of squeezing through the holes.

The data obtained from the field experiment were analyzed with nonparametric statistics (Table 27); the four-night group means are given in Table 28. No significant differences were present in either the main effects of juvenile sex or adult class, and the juvenile sex x adult class interaction was also nonsignificant (Table 27). Therefore, under field enclosure conditions, the four-night mean per cent time juveniles spent in the resident area during the active period was not significantly influenced by the sex of juveniles or the sex of adults/reproductive stage of adult females. However, there was a slight tendency for juvenile females to spend less time within enclosures occupied by nonlactating or lactating females compared to enclosures containing adult males or the control condition of no adult. No such tendency was apparent for juvenile males.

The back transformed four-night and nightly group means of the time juveniles spent in the resident area during the active period in the laboratory experiment are given in Table 28. These measures were

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Table 25. Chi square analysis of the proportions of juveniles that remained in the resident area during all four nights of the experimental test period.

	Remained for 100% of the Time	Did Not Remain for 100% of the Time
Field	26	14
Lab	4	36

$\chi^2 = 25.8133$, df = 1, $.005 > P$

Table 26. Summary of the passage tunnel and/or feeder tunnel use by juveniles prior to the placement of restraining grids during the pretest period.

	N	Used Apparatus	Did Not Use Apparatus
Field	40	39	1
Lab	40	40	0

Table 27. Nonparametric analyses of the four-night mean per cent time juveniles were in the resident area during the field experiment.

Comparison	Test	W_n or H/D Value	Prob.
Juvenile	Wilcoxin's rank-sum test	$W_n = 25$	$P > .1$
Adult	Kruskal-Wallis test	H/D = 1.6232	$.9 > P > .5$
Juvenile x Adult Interaction	Kruskal-Wallis test	H/D = 0.2666	$.975 > P > .9$

Table 28. The per cent time juveniles spent in the resident area during the active period (N = 5).

	Juvenile Male				Juvenile Female			
Adult:	Male	Nonlactating Female	Lactating Female	Control (No Adult)	Male	Nonlactating Female	Lactating Female	Control (No Adult)
				Field Experiment				
Four-night $\bar{x}$	92.0 (4)[a]	90.0 (2)	84.9 (4)	89.5 (4)	91.8 (2)*	71.8 (3)	71.7 (3)	98.2 (4)
				Laboratory Experiment				
Four-night $\bar{x}$	72.9[b] (31.1-98.7)	86.3 (54.1-99.9)	10.6 (1.4-26.8)	67.9 (42.7-99.2)	62.2 (35.9-85.1)	26.2 (0.1-80.0)	43.3 (0.4-97.4)	46.7 (19.9-74.6)
Day 1	62.2 (14.5-98.0)	91.8 (74.3-100.0)	40.9 (5.4-93.5)	59.0 (12.5-96.8)	60.9 (40.6-79.4)	32.4 (0.0-82.0)	70.0 (17.6-100.0)	76.0 (50.0-94.4)
Day 2	74.2 (31.0-99.3)	86.4 (50.3-99.9)	0.04 (0.0-24.0)	78.2 (36.3-99.8)	63.7 (38.0-85.8)	22.9 (0.0-77.2)	36.4 (0.0-92.4)	62.7 (27.2-91.8)
Day 3	78.9 (34.1-100.0)	84.9 (43.8-99.8)	0.009 (0.0-0.5)	63.5 (0.10-99.8)	69.1 (0.3-96.6)	22.5 (0.0-81.6)	31.7 (0.0-92.3)	37.5 (0.0-86.7)
Day 4	62.6 (18.2-96.6)	82.5 (44.5-99.9)	0.001 (0.0-0.1)	69.4 (25.0-98.4)	59.8 (17.8-94.4)	23.6 (0.0-82.0)	29.4 (0.0-92.1)	25.7 (12.8-41.2)

*N = 4 due to equipment malfunction.
a = number of juveniles that spent 100% of the time in the resident area.
b = back transformed mean (95% C.L.).

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evaluated by analysis of variance after the individual scores for each replication were transformed to the arcsin scale. The tables and figures showing the differences among means give the transformed values.

The four-night mean main effect of juvenile sex was not significant, but the mean main effect of adult class had a significant F-value ($.05 > P > .025$, Table 29). Inspection of Table 30 reveals that juveniles spent less time in the presence of lactating females compared to the remaining adult classes. Statistical examination of the adult class main effect was not conducted because the juvenile sex x adult class interaction was also significant ($.025 > P > .01$, Table 29). Analysis of the simple main effects indicated that the adult class main effect was significant for juvenile males ($.005 > P > .001$, Table 29), but not for juvenile females. A Student-Newman-Keuls _a posteriori_ test showed that juvenile males spent a smaller percentage of the active period in the resident area with lactating females compared to adult males, nonlactating females, and the control condition with no adult ($.01 < P$, Figure 8). Also, juvenile males spent more time with nonlactating females than did juvenile females ($P \approx .005$, Table 29). These means are graphed in Figure 9.

In conclusion for the laboratory experiment, the amount of time juveniles spent in the resident area during the active period was influenced by both the sex of juveniles and the sex of adults/reproductive stage of adult females, but the significant statistical interaction indicated that the effects were not consistent for either the juvenile or adult social factors. In respect to the juvenile sexes, males spent significantly more time with nonlactating females than did the juvenile females, but males and females spent similar amounts of time with adult

Table 29. Analysis of variance of the four-night mean per cent time juveniles spent in the resident area during the laboratory experiment.

Source of Variation	df	MSS	F-value	Prob.
Juvenile	1	735.3920	1.9228	.25 > P > .1
Adult	3	1,218.0712	3.1849	.05 > P > .025
Juvenile x Adult	3	1,499.7718	3.9214	.025 > P > .01
Error	32	382.4571		
Total	39	(SS = 21,127.5486)		
Simple Main Effects of Juvenile For:				
Adult Male	1	108.9000	0.2849	.75 > P > .5
Nonlactating Female	1	3,513.7503	9.1873	P ≃ .005
Lactating Female	1	1,228.5506	3.2123	.1 > P > .05
No Adult	1	383.1610	1.0018	.5 > P > .25
Simple Main Effects of Adult For:				
Juvenile Male	3	2,335.7062	6.1071	.005 > P > .001
Juvenile Female	3	382.2766	1.0000	.5 > P > .25
Error	32	382.4571		

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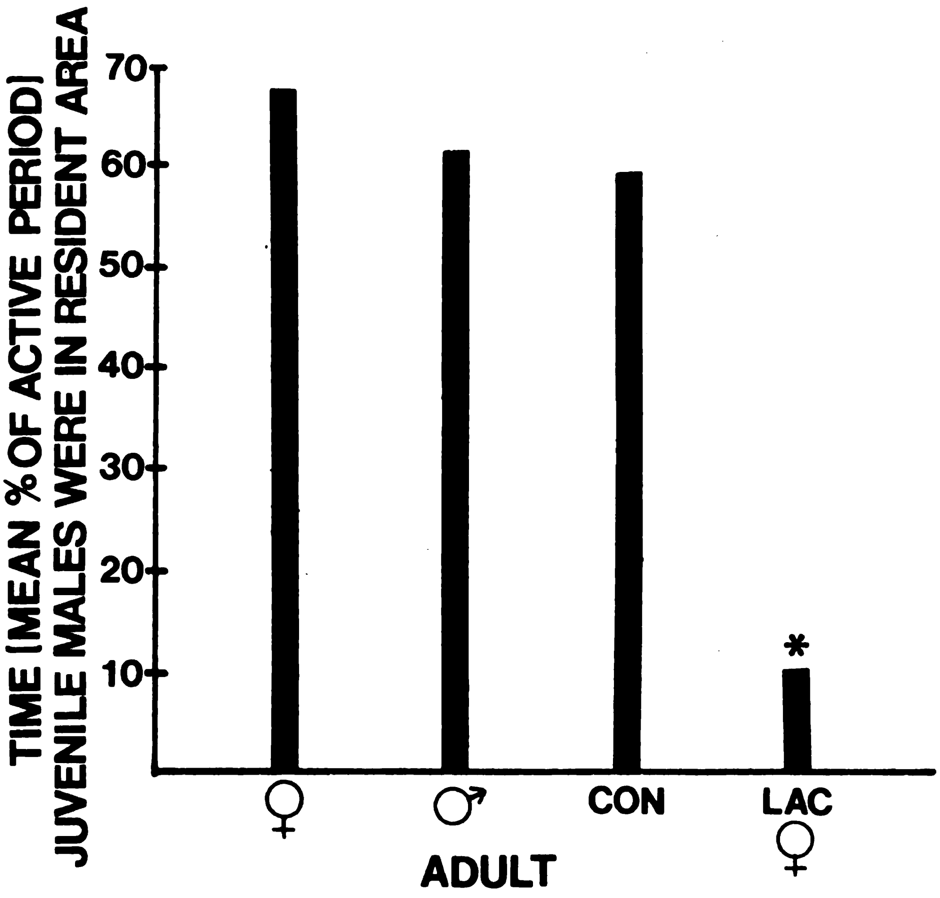
Table 30. Mean per cent time juveniles spent in the resident area for each of the adult classes during the laboratory experiment (N = 10).

Adult	*Four-night $\bar{x}$	1st Night	*2nd Night	*3rd Night	*4th Night
Male	55.4	51.7	56.2	59.4	51.5
Nonlactating Female	49.5	54.0	48.5	47.7	47.2
Lactating Female	30.5	48.3	24.0	19.8	19.2
Control with No Adult	49.3	55.4	57.3	45.3	43.4

* = significant difference among means.

Figure 8. The four-night group means for the per cent time juvenile males spent in the resident area during the laboratory experiment. The mean marked by the asterisk (*) is significantly different from the other means at the .01 level (N = 5).


TIME (MEAN % OF ACTIVE PERIOD)
JUVENILE MALES WERE IN RESIDENT AREA
70
60
50
40
30
20
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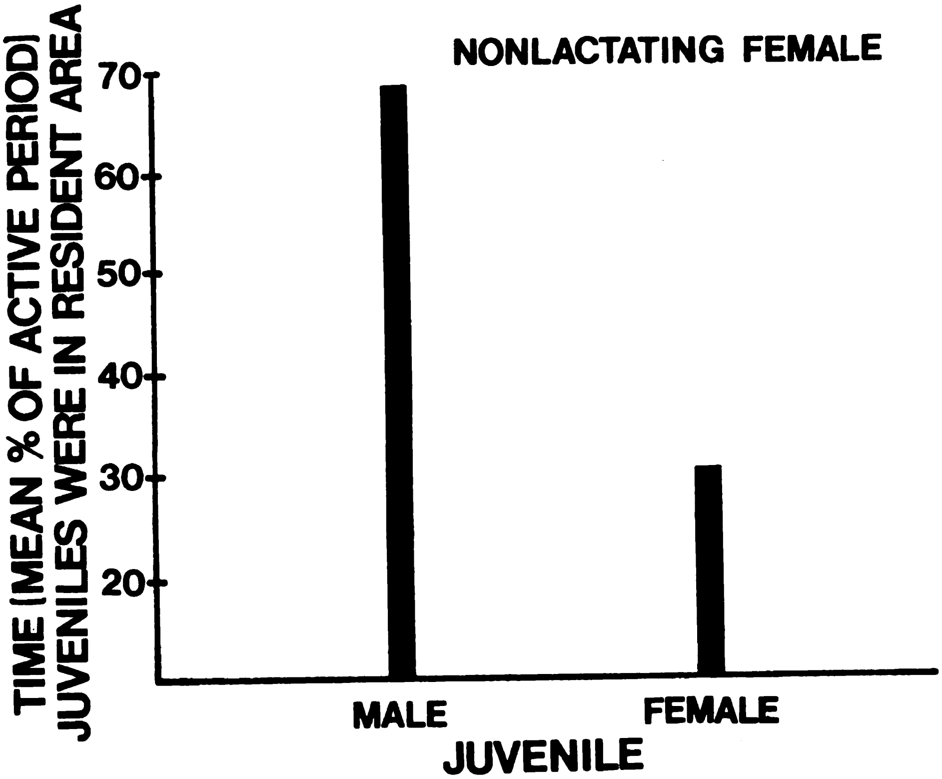
CON
LAC
♀
ADULT

Figure 8.

Figure 9. Graph showing the significant difference (P ≈ .005) in the four-night mean per cent time juvenile males and females spent in the resident area occupied by nonlactating females in the laboratory experiment (N = 5).


NONLACTATING FEMALE
TIME (MEAN % OF ACTIVE PERIOD) JUVENILES WERE IN RESIDENT AREA
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60
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MALE
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Figure 9.

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males, lactating females, and in the control condition with no adult. In respect to the adult classes, the overall main effect had a significant F-value, and inspection of the adult class treatment means revealed that juveniles spent less time with lactating females than with adult males, nonlactating females, and in the control condition with no adult. Analysis of the simple main effects and a posteriori testing showed that only juvenile males, and not juvenile females, spent significantly less time with the lactating females compared to the remaining adult classes.

In order to determine if the effects of the social factors were consistent over four-night test periods during the laboratory experiment, the nightly per cent time values were evaluated with separate analyses of variance (first night, Table 31; second night, Table 32; third night, Table 33; and fourth night, Table 34). The main effect of juvenile sex was not significant on any of the four test nights, but there was a significant adult class main effect on the last three nights ($.025 > P$). These means are given in Table 30, and it can be seen that juveniles spent less time with lactating females, compared with the remaining adult classes, during the last three nights. Statistical examination of the nightly adult class main effects was not conducted because each of the nightly juvenile sex x adult class interactions were also significant ($.05 > P$).

Analysis of the simple main effects showed that differences due to the adult classes were significant for juvenile males, but not juvenile females, on the last three nights. An a posteriori Student-Newman-Keuls test showed that on these nights juvenile males spent less time in the resident area with lactating females compared to the time spent with

Table 31. Analysis of variance of the per cent time juveniles spent in the resident area on the first night during the laboratory experiment.

Source of Variation	df	MSS	F-value	Prob.
Juvenile	1	88.2981	0.1966	.75 > P > .50
Adult	3	98.6867	0.2197	P > .75
Juvenile x Adult	3	1,547.0618	3.4445	.05 > P > .025
Error	32	449.1407		
Total	39	(SS = 19,398.0445)		
Simple Main Effects of Juvenile For:				
Adult Male	1	1.6000	0.0036	P > .75
Nonlactating Female	1	3,727.2164	8.2985	.01 > P > .005
Lactating Female	1	725.0523	1.6143	.25 > P > .10
No Adult	1	275.6250	0.6137	.5 > P > .25
Simple Main Effects of Adult For:				
Juvenile Male	3	992.3585	2.2095	.25 > P > .10
Juvenile Female	3	653.5388	1.4551	P = .25
Error	32	449.1407		

Table 32. Analysis of variance of the per cent time juveniles spent in the resident area on the second night during the laboratory experiment.

Source of Variation	df	MSS	F-value	Prob.
Juvenile	1	557.9343	1.3059	.5 > P > .25
Adult	3	2,401.5095	5.6210	.005 > P > .001
Juvenile x Adult	3	1,819.5864	4.2590	.025 > P > .01
Error	32	427.2366		
Total	39	(SS = 26,892.7915)		
Simple Main Effects of Juvenile For:				
Adult Male	1	106.2760	0.2488	.75 > P > .5
Nonlactating Female	1	3,950.1563	9.2458	.005 > P > .001
Lactating Female	1	1,718.7210	4.0229	.1 > P ≈ .05*
No Adult	1	241.5723	0.5654	.5 > P > .25
Simple Main Effects of Adult For:				
Juvenile Male	3	3,505.2879	8.2046	.001 > P
Juvenile Female	3	715.7218	1.6752	.25 > P > .10
Error	32	427.2366		

* Indicates borderline significance where the calculated value was within 0.20 units of the critical value.

Table 33. Analysis of variance of the per cent time juveniles spent in the resident area on the third night during the laboratory experiment.

Source of Variation	df	MSS	F-value	Prob.
Juvenile	1	614.0290	1.0776	.5 > P > .25
Adult	3	2,783.5504	4.8850	.01 > P > .005
Juvenile x Adult	3	1,975.7248	3.4673	.05 > P > .025
Error	32	569.8143		
Total	39	(SS = 33,125.9108)		
Simple Main Effects of Juvenile For:				
Adult Male	1	103.4266	0.1815	.75 > P > .50
Nonlactating Female	1	3,770.5872	6.6172	.025 > P > .01
Lactating Female	1	2,099.8908	3.6852	.1 > P > .05
No Adult	1	567.0090	0.9951	.5 > P > .25
Simple Main Effects of Adult For:				
Juvenile Male	3	4,035.6675	7.0824	.001 > P
Juvenile Female	3	723.6400	1.2700	.5 > P > .25
Error	32	569.8143		

Table 34. Analysis of variance of the per cent time juveniles spent in the resident area on the fourth night during the laboratory experiment.

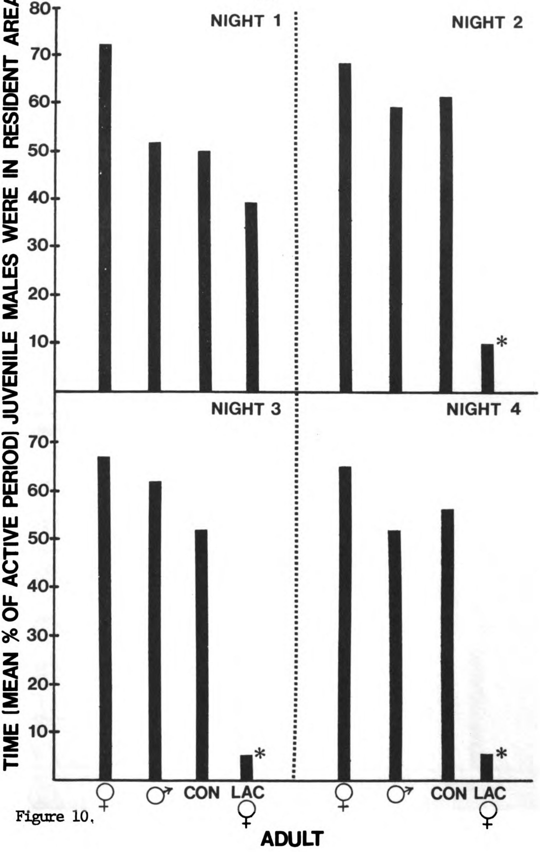
Source of Variation	df	MSS	F-value	Prob.
Juvenile	1	834.2082	1.7865	.25 > P > .10
Adult	3	2,086.6736	4.4686	.025 > P > .01
Juvenile x Adult	3	1,994.5878	4.2714	.025 > P > .01
Error	32	466.9589		
Total	39	(SS = 28,020.6784)		
Simple Main Effects of Juvenile For:				
Adult Male	1	6.8724	0.0147	P > .75
Nonlactating Female	1	3,275.3760	7.0143	.025 > P > .01
Lactating Female	1	1,855.5888	3.9738	.1 > P > .05
No Adult	1	1,680.1344	3.5980	.1 > P > .05
Simple Main Effects of Adult For:				
Juvenile Male	3	3,575.7644	7.6576	.001 > P
Juvenile Female	3	505.4971	1.0825	.5 > P > .25
Error	32	466.9589		

adult males, nonlactating females, and the control condition with no adult (.01 > P). These differences are graphed in Figure 10, and the results for the first night are given for comparison. Juvenile males, compared with juvenile females, spent more time with nonlactating females on all four nights (.025 > P, Figure 11). On the second night, juvenile females spent more time in the resident area with lactating females than did juvenile males; this difference closely approached significance (Table 32). These data, and the comparisons for the remaining nights, are given in Figure 12.

It is apparent that, subsequent to the first night, the significant differences due to the main effect of the adult classes were consistent with the analysis of the overall four-night means. The difference between the juvenile sexes for nonlactating females was consistent on all four nights. Finally, the effects of the social factors in general were consistent over nights since only one comparison, juvenile sex for lactating females, showed a difference (but not significant) which was not found in the analysis of the four-night mean values.

In summary, the analyses of the three settlement measures obtained in the field and laboratory experiments indicate that both the sex of juveniles and the sex of adults/reproductive stage of adult females may affect the outcome of juvenile-adult social interactions. Therefore, both juvenile and adult social factors may influence settlement. Inspection of Table 35 reveals two major points concerning the effects of social factors. Firstly, the outcomes of juvenile-adult social interactions were not consistent in the field and laboratory experiments. This is indicated by the failure to detect similar patterns of significant differences among social factors in the analyses of the

Figure 10. Nightly means of the per cent time juvenile males spent in the resident area during the laboratory experiment. The asterisk (*) indicates a significantly different mean at the .01 level (N = 5).


TIME (MEAN % OF ACTIVE PERIOD) JUVENILE MALES WERE IN RESIDENT AREA
80
70
60
50
40
30
20
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NIGHT 1
NIGHT 2
*
NIGHT 3
NIGHT 4
70
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50
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30
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CON
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CON
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ADULT

Figure 10.

Figure 11. Graph showing the significant differences (.025 > P) in the nightly comparisons of the mean per cent time juvenile males and females spent in the resident areas occupied by nonlactating females during the laboratory experiment (N = 5 for each night).

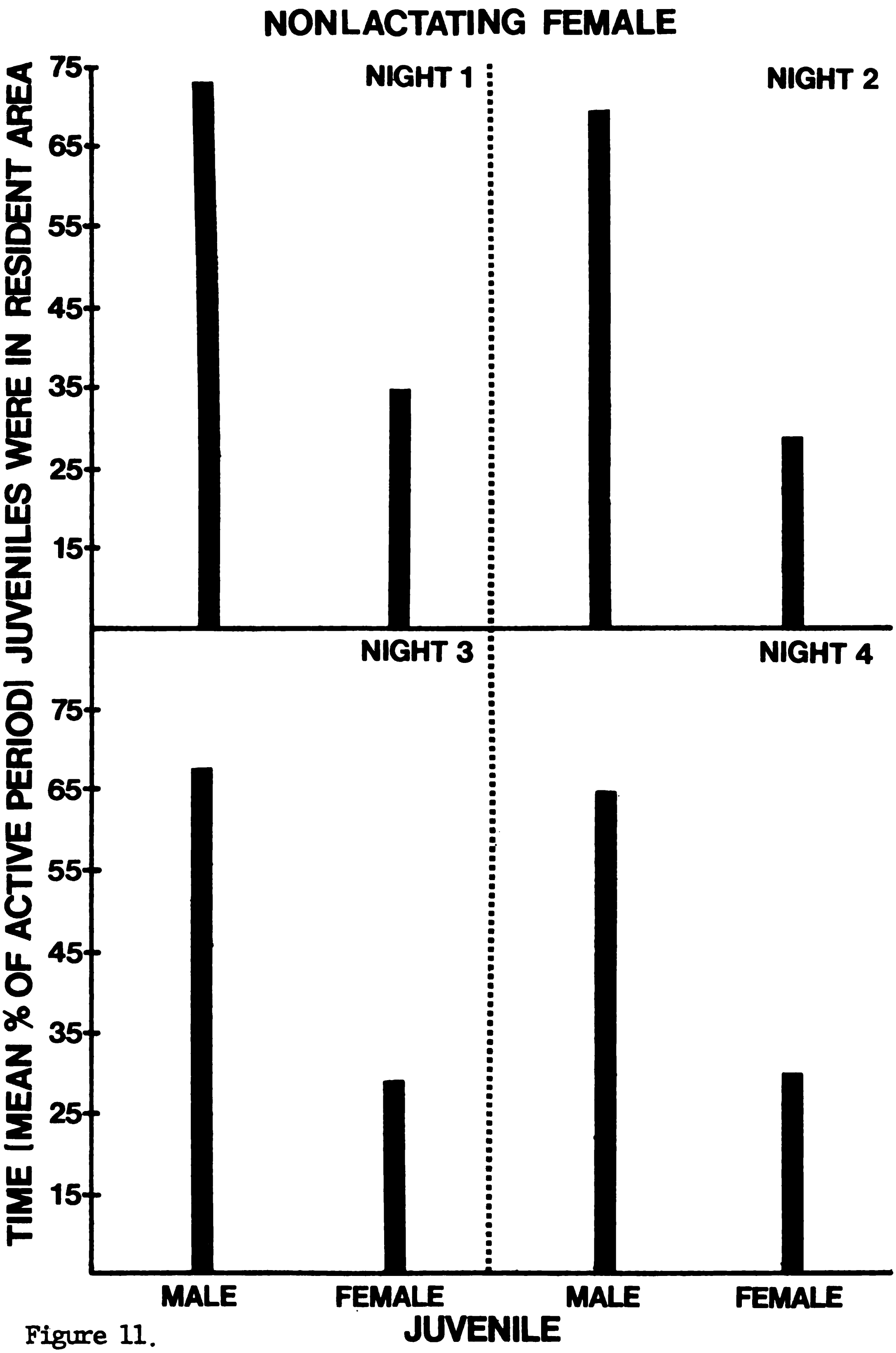
NONLACTATING FEMALE
NIGHT 1
NIGHT 2
NIGHT 3
NIGHT 4
TIME (MEAN % OF ACTIVE PERIOD) JUVENILES WERE IN RESIDENT AREA
75
65
55
45
35
25
15
MALE
FEMALE
MALE
FEMALE
JUVENILE

Figure 11.

Figure 12. Nightly comparisons of the mean per cent time juvenile males and females spent in the resident areas occupied by lactating females during the laboratory experiment (N = 5).

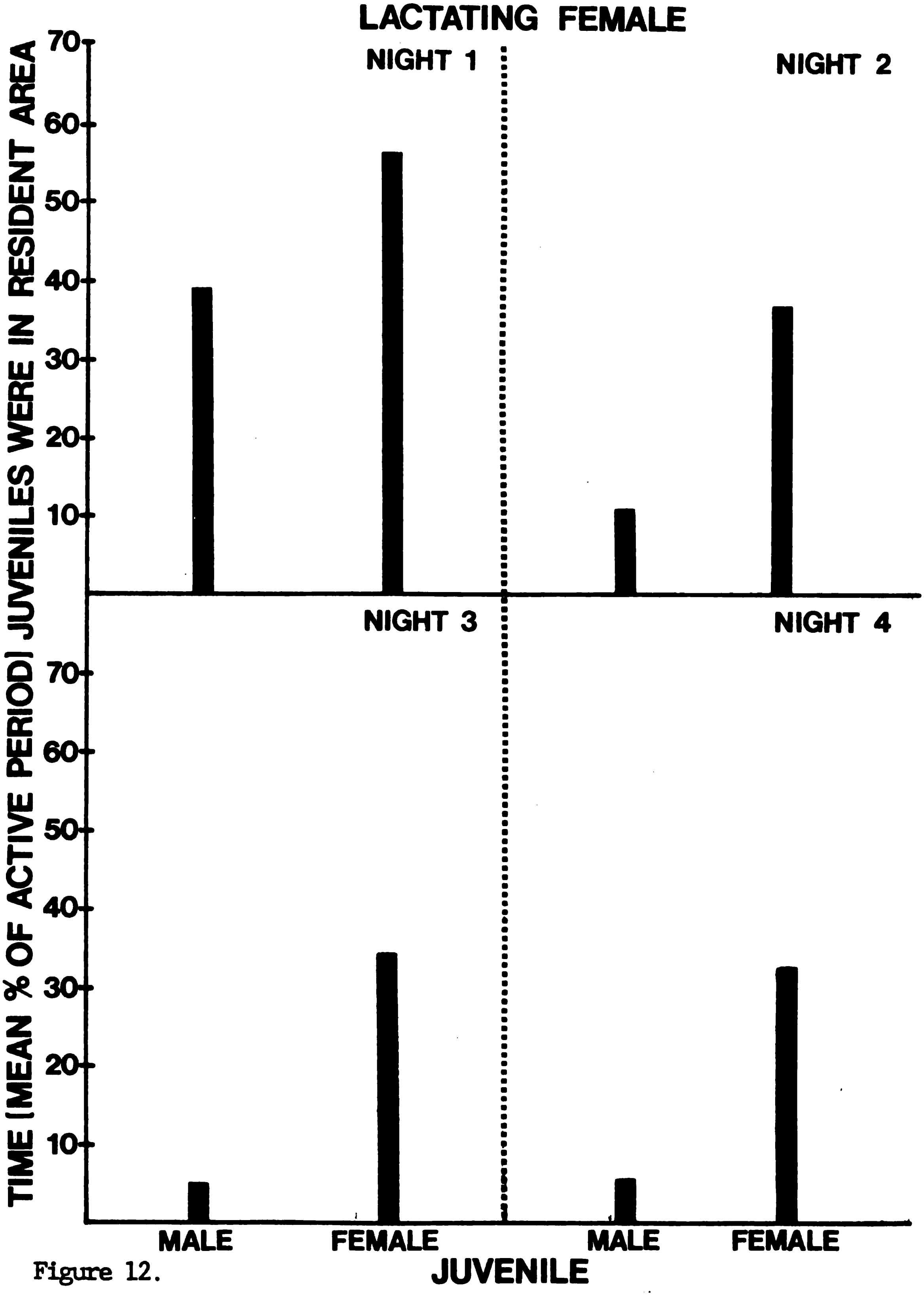
LACTATING FEMALE
NIGHT 1
NIGHT 2
NIGHT 3
NIGHT 4
TIME (MEAN % OF ACTIVE PERIOD) JUVENILES WERE IN RESIDENT AREA
70
60
50
40
30
20
10
MALE
FEMALE
MALE
FEMALE
JUVENILE

Figure 12.

Table 35. Summary of the analyses of the three settlement variables.

Settlement Dependent Variables	Main Effect		Interaction
	Juvenile Sex	Adult Class	
Field Experiment			
Nesting location*	-	-	-
Nesting arrangement*	o	o	+
Per cent time in Resident area (a)	-	-	-
Laboratory Experiment			
Nesting location*	o	o	+
Nesting arrangement*	o	o	+
Per cent time in Resident area (b)	-	+	+

* = chi square test.
(a) = nonparametric test.
(b) = analysis of variance.
\+ = significant social factor main or interaction effect.
\- = nonsignificant.
o = test was not made because statistical interaction was present.

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field and laboratory data. Secondly, the significant statistical interactions between juvenile sexes and adult classes show that, in these cases, juvenile sexes differed in their response towards the various adult classes. A summary of the significant statistical interactions is given in Table 36.

The sex of juveniles significantly affected the settlement measures only when nonlactating females were encountered. Juvenile females, compared with juvenile males, nested with nonlactating females less frequently in the field experiment and spent less time within the enclosures occupied by nonlactating females in the laboratory experiment. Also, in respect to the juvenile sexes, juvenile males tended to nest within enclosures occupied by nonlactating females in the laboratory ($P \simeq .065$). The sex of adults/reproductive stage of adult females significantly affected the settlement measures only for juvenile males during the laboratory experiment. These juveniles nested less frequently and spent less time within enclosures containing lactating females compared to those containing adult males, nonlactating females, or the control condition with no adult. There was some evidence to indicate that juvenile females nested more frequently with adult males than with nonlactating females or lactating females in the field experiment ($P \simeq .07$). Also, both juvenile sexes tended to nest with lactating females less frequently than with adult males or nonlactating females in the laboratory ($P \simeq .06$).

On the basis of these results, it can be concluded that adult females may limit the settlement of juveniles in P. m. bairdi. However, the limitation is dependent upon the sex of juveniles and upon the reproductive stage of adult females. Compared with juvenile males,

Table 36. Summary of the analyses of the significant statistical interactions between juvenile sexes and adult classes for the three settlement variables.

Comparison	Dependent Variable/Experiment			
	Nesting Location/ Laboratory	Nesting Arrangement/ Field	Nesting Arrangement/ Laboratory	Four-Night Mean Per Cent Time in Resident Area/ Laboratory
Juvenile sex for:				
Adult male	-	-	-	-
Nonlactating female	# 9^a	+ 16^a	-	+ 9^b
Lactating female	-	-	o	-
Control condition	-	o	o	-
Adult class for:				
Juvenile male	+ 12^a	-	-	+ 8^b
Juvenile female	-	# 19^a	-	-
Pooled juvenile male and female	o	o	# 24^a	o

a = table showing significant difference.
b = figure showing significant difference.
o = test was not made.

+ = significant simple main effect.
- = nonsignificance.
= borderline alpha level where $.07 \geq P > .05$.

juvenile females may be limited by nonlactating females. Compared with adult males and nonlactating females, lactating females may limit the settlement of juvenile males. Also, nonlactating and lactating females, compared with adult males, may limit the settlement of juvenile females, but the evidence is not conclusive. The present study provided no evidence to indicate that adult males limit the settlement of juvenile males or juvenile females to a greater degree than either nonlactating or lactating females. Finally, the physical environment appeared to be an important factor in determining the effects of social factors on the juvenile settlement measures.

<u>Activity Between the Resident and Dispersal Areas</u>. The juvenile activity in the passage tunnel, expressed as the number of passage tunnel trips per hour of the active period, was examined in order to determine if social conditions influenced the rate at which juveniles entered and left the resident area. As was pointed out previously, a smaller proportion of juveniles used the passage tunnels in the field experiment compared to the laboratory experiment (.005 > P, Table 25).

The data obtained from the field experiment were analyzed with nonparametric statistics (Table 37); the four-night group means are given in Table 38. No significant differences were found for the main effects of juvenile sex or adult class, and the juvenile sex x adult class interaction was nonsignificant as well (Table 37). The results above indicate that the social conditions did not affect the rate of juvenile activity between areas in the field-enclosure experiment. This finding is consistent with the failure to detect differences among treatment groups for the amount of time juveniles spent in the resident area.

Table 37. Nonparametric analysis of the four-night mean juvenile activity rate in the passage tunnel during the field experiment.

Comparison	Test	W_n or H/D Value	Prob.
Juvenile	Wilcoxin's rank-sum test	$W_n = 25$	$P > .1$
Adult	Kruskal-Wallis test	$H/D = 1.6224$	$.9 > P > .5$
Juvenile x Adult Interaction	Kruskal-Wallis test	$H/D = 0.6812$	$.9 > P > .5$

The back transformed four-night and nightly group means of the juvenile activity rate obtained in the laboratory experiment are given in Table 38. These measures were evaluated by analysis of variance after the individual raw scores for each replication were transformed to the $\sqrt{y + 1/2}$ scale. The tables and figures showing the differences among means give the transformed values.

The four-night mean main effect of adult class had a significant F-value ($.05 > P > .025$), but the juvenile sex main effect and the juvenile sex x adult class interaction were nonsignificant (Table 39). The adult treatment group means are given in Table 40. Juvenile activity was significantly higher when juveniles encountered adult males compared to lactating females (Student-Newman-Keuls test, $.05 > P$, Table 41). None of the other comparisons was significantly different. Figure 13 shows the magnitudinal relationships among the four-night adult treatment means.

The nightly activity rates were evaluated with separate analyses of variance to determine if the effects of social factors were

Table 38. The number of passage tunnel trips per hour of the active period (N = 5).

	Juvenile Male				Juvenile Female			
Adult:	Male	Nonlactating Female	Lactating Female	Control (No Adult)	Male	Nonlactating Female	Lactating Female	Control (No Adult)
				Field Experiment				
Four-night $\bar{x}$	0.14 (4)^a	0.52 (2)	0.35 (4)	1.18 (4)	0.61 (2)*	0.80 (3)	0.11 (3)	0.35 (4)
				Laboratory Experiment				
Four-night $\bar{x}$	8.54^b (1.12-21.98)	3.16 (0.29-8.14)	1.38 (0.00-5.54)	4.57 (0.32-12.43)	10.83 (2.90-23.40)	4.79 (1.34-10.03)	5.10 (0.28-14.33)	7.85 (2.59-15.67)
Day 1	15.10 (1.91-39.99	3.37 (0.31-8.70)	1.27 (0.00-5.16)	5.41 (0.20-15.74)	13.86 (3.83-29.75)	6.74 (3.96-10.20)	5.85 (0.00-20.57)	6.62 (2.78-11.93)
Day 2	7.31 (0.90-18.90)	3.27 (0.21-8.75)	1.27 (0.00-5.40)	4.93 (0.03-14.95)	11.54 (3.61-23.64)	3.95 (0.58-9.61)	7.77 (0.00-28.29)	9.08 (1.45-22.49)
Day 3	5.27 (0.25-15.02)	2.85 (0.14-7.68)	1.54 (0.00-6.30)	4.02 (0.29-10.83)	9.88 (1.92-23.39)	3.43 (0.00-11.38)	5.79 (0.00-18.66)	5.16 (0.00-16.78)
Day 4	6.06 (0.85-15.18)	3.02 (0.19-8.01)	1.42 (0.00-5.47)	3.65 (0.49-9.00)	7.55 (1.15-18.78	4.14 (0.42-10.79	3.12 (0.04-8.90)	8.97 (3.13-17.55)

*N = 4 due to equipment malfunction.
a = number of juveniles that did not trip the passage tunnel.
b = back transformed means (95% C.L.).

Table 39. Analysis of variance of the four-night mean juvenile activity rate in the passage tunnel during the laboratory experiment.

Source of Variation	df	MSS	F-value	Prob.
Juvenile	1	3.5367	3.1722	.1 > P > .05
Adult	3	3.3633	3.0167	.05 > P > .025
Juvenile x Adult Interaction	3	0.2171	0.1948	P > .75
Error	32	1.1149		
Total	39	(SS= 35.6771)		

consistent over nights (first night, Table 42, second night, Table 43; third night, Table 44; and fourth night, Table 45). There was a significant adult class main effect on the first night only (.01 > P > .005, Table 42). The juvenile sex main effect and juvenile sex x adult class interaction were never significant. An *a posteriori* Student-Newman-Keuls test on the adult treatment means for the first night showed that juveniles moved more frequently between the resident and dispersal areas when adult males were encountered compared to nonlactating females, the control condition (.05 > P), and lactating females (.01 > P, Table 46). The latter three group means were not significantly different. Figure 14 shows the magnitudinal relationships among the adult treatment means for the first test night.

The results show that the significant differences among the four-night mean activity rates can be attributed to the significant differences among the adult classes on the first test night. There were significant differences among treatment groups for the amount of time

Table 40. Mean (± 1 S.E.) juvenile activity rate in the passage tunnel for each of the adult classes during the laboratory experiment (N = 10).

Adult	*Four-night $\bar{x}$	*1st Night	2nd Night	3rd Night	4th Night
Male	3.19 ± 0.40	3.87 ± 0.50	3.13 ± 0.38	2.81 ± 0.41	2.70 ± 0.36
Nonlactating Female	2.11 ± 0.25	2.33 ± 0.24	2.03 ± 0.26	1.91 ± 0.30	2.02 ± 0.27
Lactating Female	1.87 ± 0.35	1.93 ± 0.44	2.10 ± 0.53	1.97 ± 0.42	1.64 ± 0.28
Control With No Adult	2.57 ± 0.32	2.55 ± 0.31	2.71 ± 0.42	2.25 ± 0.14	2.56 ± 0.32

* Indicates that significant differences exist among a group of means.

Table 41. Student-Newman-Keuls test for differences among the four-night adult class means of juvenile activty rate in the passage tunnel during the laboratory experiment.

Adult	Four-Night Mean ± 1 S.E.	*	*
Male	3.19 ± 0.40	|	
Control	2.57 ± 0.32	|	|
Nonlactating Female	2.11 ± 0.25	|	|
Lactating Female	1.87 ± 0.35		|

*Any two means (± 1 S.E.) not joined by the same vertical line are significantly different at .05 > P (N = 10).

Figure 13. Four-night adult group means for the juvenile activity rate in the passage tunnel during the laboratory experiment. The vertical lines indicate ± 1 S.E. (N = 10).

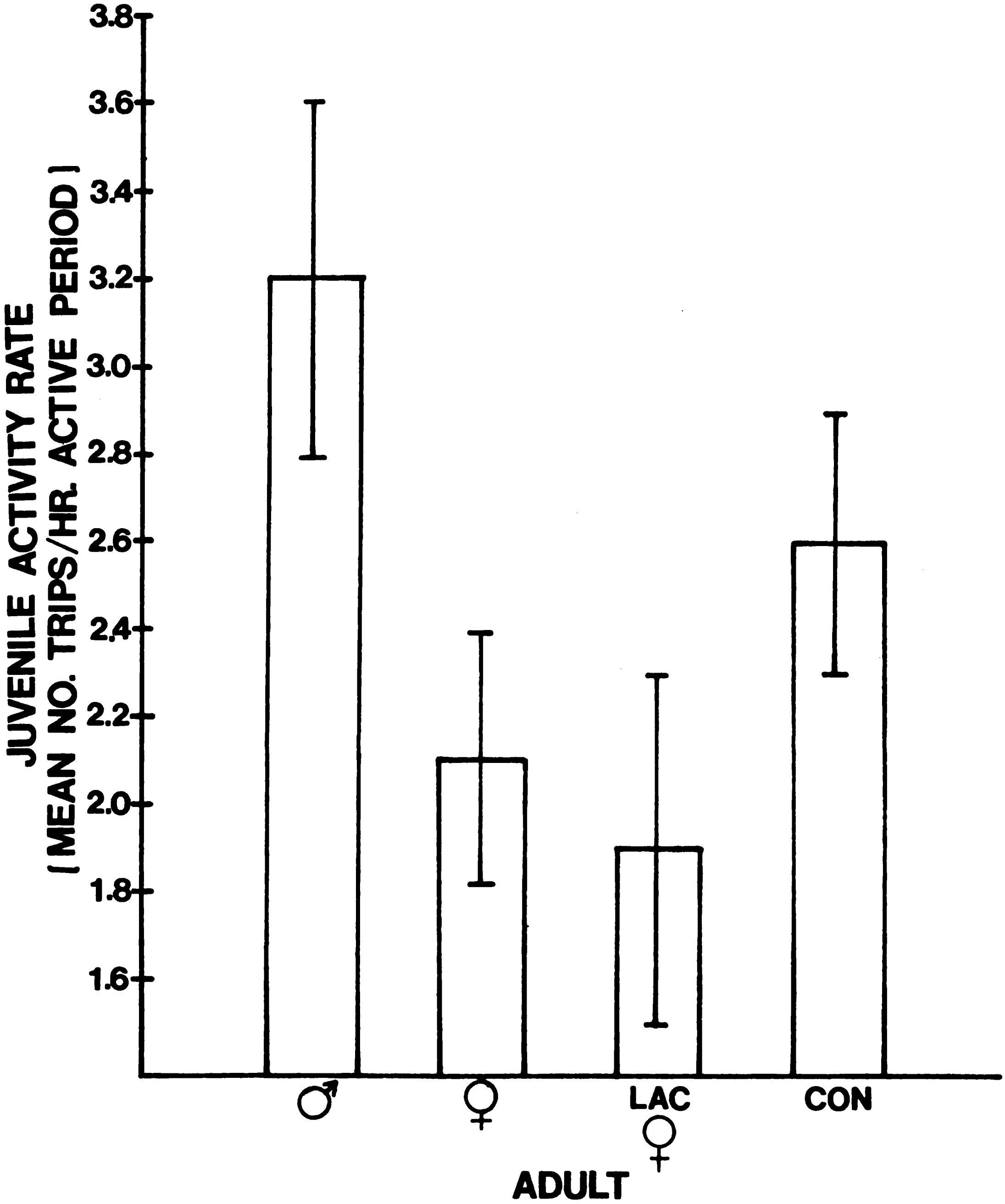
JUVENILE ACTIVITY RATE
(MEAN NO. TRIPS/HR. ACTIVE PERIOD)
3.8
3.6
3.4
3.2
3.0
2.8
2.6
2.4
2.2
2.0
1.8
1.6
♂
♀
LAC ♀
CON
ADULT

Figure 13.

Table 42. Analysis of variance of the juvenile activity rate in the passage tunnel on the first night during the laboratory experiment.

Source of Variation	df	MSS	F-value	Prob.
Juvenile	1	2.4572	1.6052	.25 > P > .1
Adult	3	7.1087	4.6439	.01 > P > .005
Juvenile x Adult Interaction	3	0.8657	0.5655	.75 > P > .5
Error	32	1.5308		
Total	39	(SS = 75.3647)		

Table 43. Analysis of variance of the juvenile activity rate in the passage tunnel on the second night during the laboratory experiment.

Source of Variation	df	MSS	F-value	Prob.
Juvenile	1	6.2110	3.8585	.1 > P > .05
Adult	3	2.7589	1.7139	.25 > P > .1
Juvenile x Adult Interaction	3	0.8108	0.5037	.75 > P > .5
Error	32	1.6097		
Total	39	(SS = 68.4305)		

Table 44. Analysis of variance of the juvenile activity rate in the passage tunnel on the third night during the laboratory experiment.

Source of Variation	df	MSS	F-value	Prob.
Juvenile	1	3.3126	2.2781	.25 > P > .1
Adult	3	1.7124	1.1776	.5 > P > .25
Juvenile x Adult Interaction	3	0.4986	0.3429	P > .75
Error	32	1.4541		
Total	39	(SS = 56.4776)		

Table 45. Analysis of variance of the juvenile activity rate in the passage tunnel on the fourth night during the laboratory experiment.

Source of Variation	df	MSS	F-value	Prob.
Juvenile	1	2.7794	2.8971	P ≃ .1
Adult	3	2.3943	2.4957	.1 > P > .05
Juvenile x Adult Interaction	3	0.3231	0.3367	P > .75
Error	32	0.9594		
Total	39	(SS = 41.6317)		

Table 46. Student-Newman-Keuls test for differences among the first night adult class means of juvenile activity rate in the passage tunnel during the laboratory experiment.

Adult	Mean (±1 S.E.)			
Male	3.87 ± 0.50		+	
Control	2.55 ± 0.31	*	│	+
Nonlactating Female	2.33 ± 0.24	│	│	│
Lactating Female	1.93 ± 0.44	│		│

Note: Any two means (±1 S.E.) not joined by the same vertical line are significantly different at $.05 > P^*$ or $.01 > P^+$.

Figure 14. First night adult group means of the juvenile activity rate in the passage tunnel during the laboratory experiment. The vertical lines indicate ± 1 S.E. (N = 10).

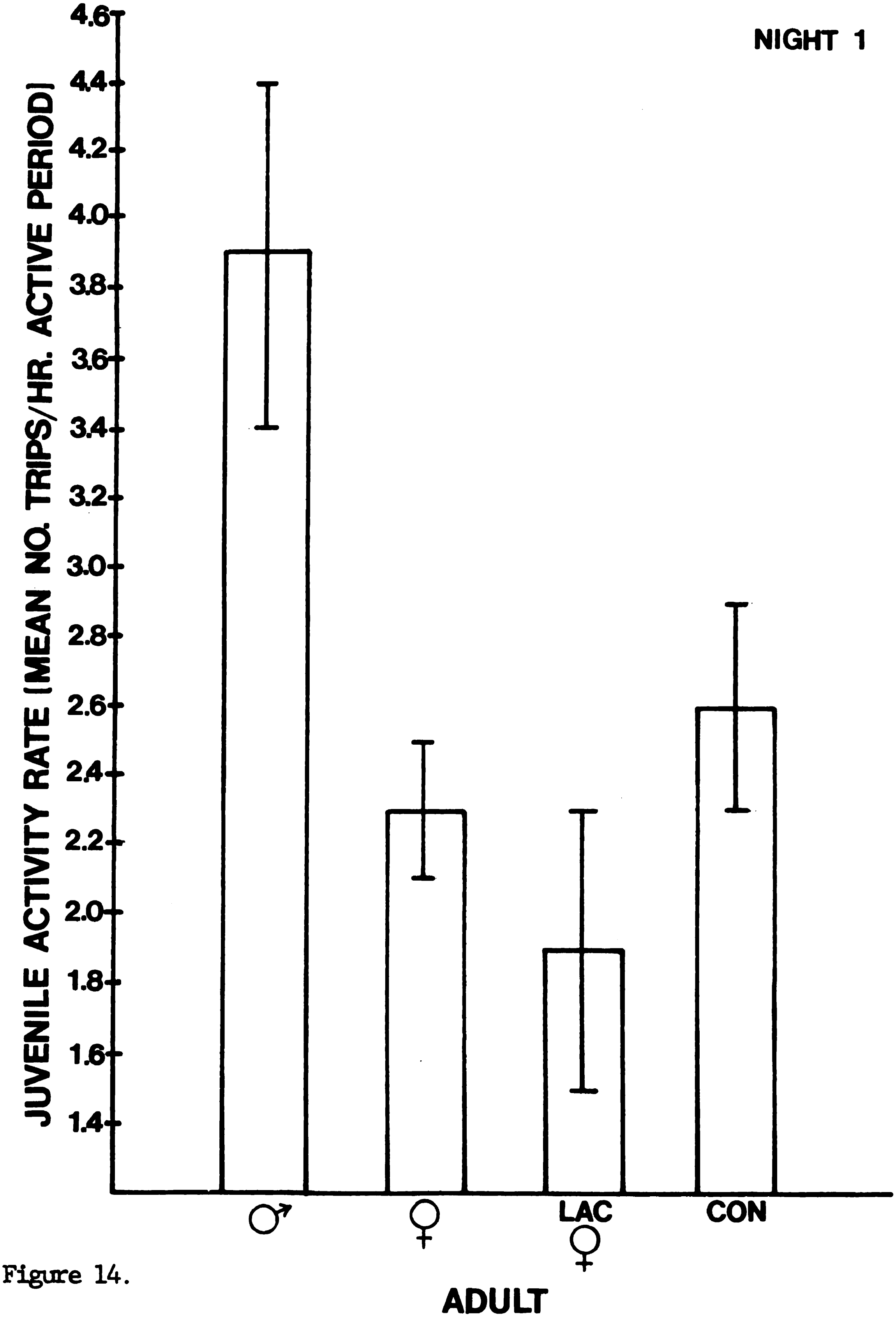
NIGHT 1
JUVENILE ACTIVITY RATE (MEAN NO. TRIPS/HR. ACTIVE PERIOD)
4.6
4.4
4.2
4.0
3.8
3.6
3.4
3.2
3.0
2.8
2.6
2.4
2.2
2.0
1.8
1.6
1.4
♂
♀
LAC ♀
CON
ADULT

Figure 14.

juveniles spent within the resident area during the last three test nights (see Tables 32, 33, and 34). The inconsistency of these results indicates that even though the amount of time juveniles spent in the resident area was affected by social conditions, the movement rate of juveniles in and out of the resident area was not affected on the last three nights. Therefore, when social conditions led to a relatively exclusive or nonexclusive use of a confined space, based on a time measure, the propensity of juveniles to enter and leave that space was not affected.

Juvenile Weight Change

Adult male P. m. austerus have been reported to retard the growth rates of juveniles under free-ranging and laboratory conditions (Healey, 1967). In an attempt to reexamine and expand upon this reported influence, the weight changes of juveniles in the present experiment were examined. No distinction was made between juveniles that always remained in the resident area and those that spent some time in the dispersal area, since dispersing juveniles in free-ranging populations may remain near resident adults or leave the residents' home ranges. A summary of the juvenile weight change group means is given in Table 47.

A 2 x 2 x 4 factorial analysis of variance was performed on the weight change data combined from the field and laboratory experiment (Table 48). Neither the juvenile sex nor adult class main effects were significant, but juveniles had higher growth rates in the field experiment than in the laboratory experiment ($.01 > P > .005$, see Figure 15). None of the interaction F-values involving the location main effect was significant, however, the juvenile sex x adult class interaction was

Table 47. Group means (± 1 S.E.) of the weight change of juveniles. Negative values indicate a mean loss of weight within a group (N = 5).

	Field Experiment		Laboratory Experiment	
	Juvenile Male	Juvenile Female	Juvenile Male	Juvenile Female
<u>Adult</u>				
Male	2.00 ± 0.66	0.02 ± 0.22	0.04 ± 0.22	-0.76 ± 0.57
Nonlactating Female	0.20 ± 0.58	0.66 ± 0.41	0.30 ± 0.41	0.62 ± 0.34
Lactating Female	0.98 ± 0.54	0.26 ± 0.38	0.74 ± 0.72	-0.12 ± 0.52
Control (No Adult)	0.14 ± 0.19	0.66 ± 0.65	-0.50 ± 0.32	-0.48 ± 0.29

significant (P ≈ .025). Table 49 shows the interaction group means. These results suggest that the physical environment of the laboratory experiment (<u>e.g.</u>, confined and sterile space, disturbance by the experimenter, etc.) may have led to a reduction in the growth rates of juveniles. But the effects of the experimental social factors appeared to be consistent between the field and laboratory experiments.

Analysis of the simple main effects of the juvenile sex x adult class interaction showed that the sex of juveniles was important only when adult males are encountered. Juvenile males had higher growth rates when interacting with adult males than did juvenile females (.005 > P > .001, Table 48). This difference is illustrated in Figure 16. Also, there was a significant F-value in the comparison of adult classes for juvenile males (.05 > P > .025, Table 48). Juvenile males had

Table 48. Analysis of variance of juvenile weight change.

Source of Variation	df	MSS	F-value	Prob.
Location	1	8.0645	7.3476	.01 > P > .005
Juvenile	1	2.8880	2.6313	.25 > P > .10
Adult	3	1.1192	1.0197	.5 > P > .25
Location x Juvenile	2	0.0500	0.0456	P > .75
Location x Adult	3	1.9218	1.7510	.25 > P > .10
Juvenile x Adult	3	3.6727	3.3462	P ≃ .025
Location x Juvenile x Adult	3	0.6840	0.6232	.75 > P > .5
Error	64	1.0976		
Total	79	(SS = 103.44)		
Simple Main Effects of Juvenile For:				
Adult Male	1	9.6605	8.8015	.005 > P > .001
Nonlactating Female	1	0.7605	0.6929	.5 > P > .25
Lactating Female	1	3.1205	2.8430	.1 > P > .05
No Adult	1	0.3645	0.3321	.75 > P > .5
Simple Main Effects of Adult For:				
Juvenile Male	3	3.0809	2.8070	.05 > P > .025
Juvenile Female	3	1.7109	1.5588	.25 > P > .10
Error	64	1.0976		

Figure 15. Graph of the significant difference between the mean weight changes for juveniles used in the field experiment and the laboratory experiment. The vertical lines indicate ± 1 S.E. (N = 40).

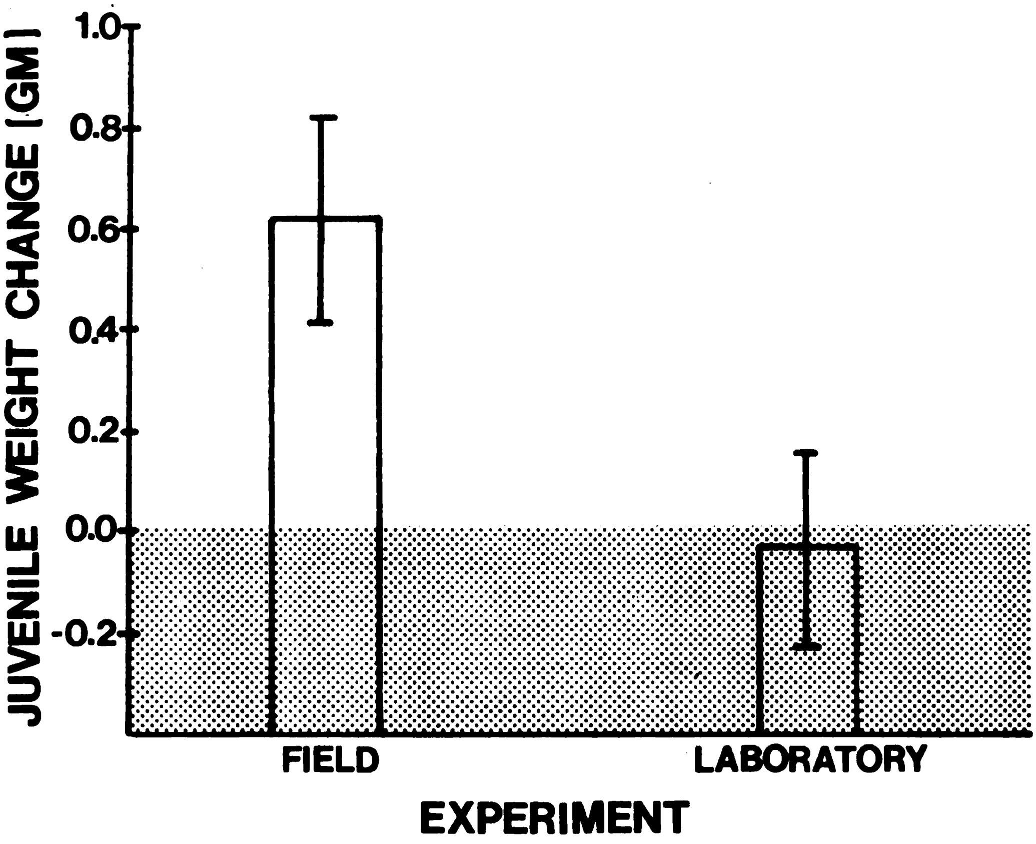
JUVENILE WEIGHT CHANGE (GM)
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
FIELD
LABORATORY
EXPERIMENT

Figure 15.

Table 49. Summary of the juvenile sex x adult class interaction group means (± 1 S.E.) of the weight change of juveniles (N = 10). Negative values indicate a mean loss of weight within a group.

Adult	Juvenile male[a]		Juvenile Female
Male	1.02 ± 0.46	*	-0.37 ± 0.32
Nonlactating Female	0.47 ± 0.31		0.64 ± 0.25
Lactating Female	0.86 ± 0.43		0.07 ± 0.31
Control With No Adult	-0.18 ± 0.20		0.09 ± 0.38

* = significant difference between juvenile sexes.
a = significant difference among adult classes.

Table 50. Student-Newman-Keuls test among adult class means (± 1 S.E.) for the weight change of juvenile males (N = 10). Negative values indicate a mean loss of weight with a group.

Juvenile Tested With		*	*
Adult Male	1.02 ± 0.46	|	
Lactating Female	0.86 ± 0.43	|	|
Nonlactating Female	0.47 ± 0.31	|	|
Control With No Adult	-0.18 ± 0.20		|

* means not connected by the same vertical line are significantly different at .05 > P.

Figure 16. Graph of the significant difference between the mean weight changes for juvenile males and juvenile females tested with adult males. The vertical lines indicate ± 1 S.E. (N = 10).

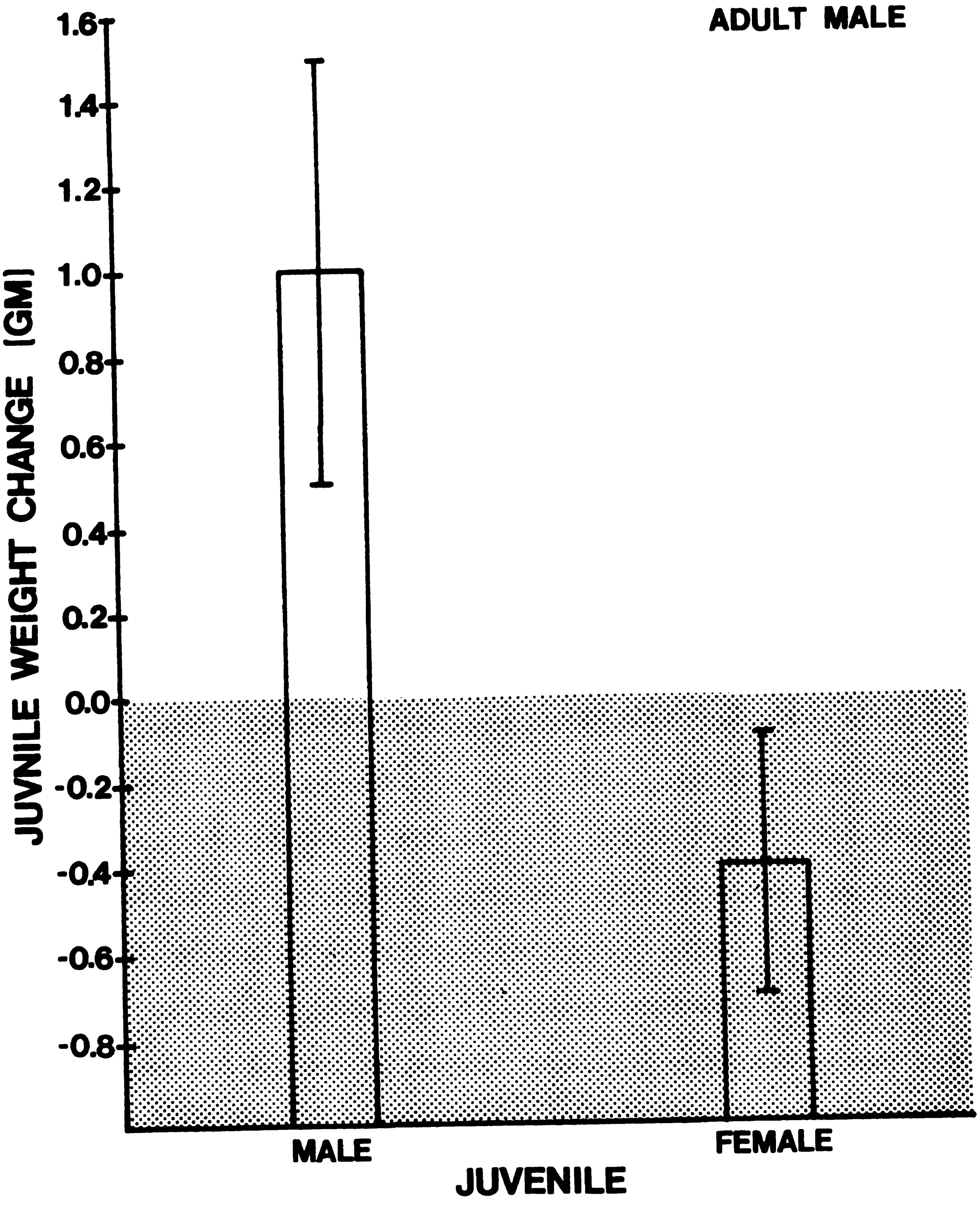
ADULT MALE
JUVNILE WEIGHT CHANGE (GM)
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
MALE
FEMALE
JUVENILE

Figure 16.

higher growth rates when adult males were encountered compared to the control condition of no adult (Student-Newman-Keuls test, .05 > P, Table 50). Figure 17 shows the differences in magnitude of these means.

In conclusion, the growth rate of juveniles was significantly influenced by their sex only when adult males were encountered. In this case, juvenile females gained less weight than did juvenile males. There were no significant differences in the effect of the adult social factors for either male or female juveniles. However, juvenile male growth rates may be inhibited by the absence of conspecifics since control juvenile males gained significantly less weight than the juvenile males that interacted with adult males.

Descriptive Measures

Wounding. Eight (40%) of the 20 juveniles tested with lactating females were wounded; one juvenile female died the day after the experiment was completed, presumably from wounds received from a lactating female. No juveniles were wounded by adult males, and only one juvenile, a female, was wounded by nonlactating females (Table 51). The fact that controls had no wounding indicates that juveniles were not lacerated while squeezing through the restraining grids. These findings support the conclusion that adult male and nonlactating female *P. m. bairdi* are not aggressive towards strange juveniles of either sex. However, lactating females are aggressive towards both male and female juveniles.

Direct Observations. The mice were observed in order to obtain measures of the frequencies of fighting, chasing, and avoidance behaviors. The number of 15-second intervals during which both the

Figure 17. Graph of the mean weight changes for juvenile males. The vertical lines indicate ± 1 S.E. (N = 10).

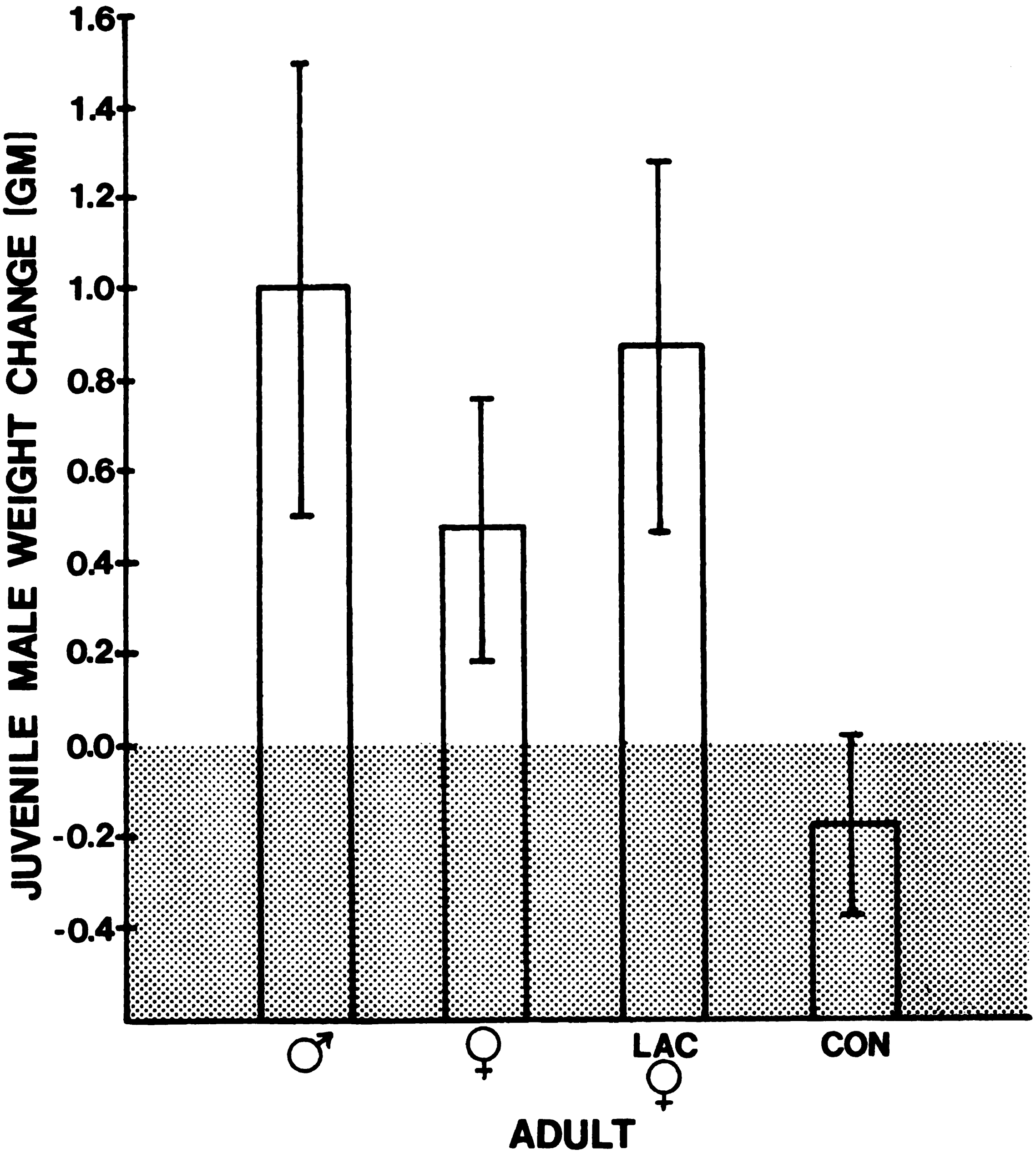
JUVENILE MALE WEIGHT CHANGE (GM)
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
♂
♀
LAC ♀
CON
ADULT

Figure 17.

Table 51. Treatment group summary of juvenile wounding (N = 5)

		Juvenile Male		Juvenile Female	
Location	Adult	No. Juveniles Wounded	Wounds/Juvenile Wounded	No. Juveniles Wounded	Wounds/Juvenile Wounded
Field	Male	0	0	0	0
	Nonlactating Female	0	0	0	0
	Lactating Female	3	2	0	0
	Control (No Adult)	0	0	0	0
Laboratory	Male	0	0	0	0
	Nonlactating Female	0	0	1	1
	Lactating Female	2	8.5	3	4.7
	Control (No Adult)	0	0	0	0

juveniles and the adults were observed in the resident area was low. Consequently, the frequencies of behaviors were too small to merit statistical analysis.

Only one fight was observed; a nonlactating female initiated a locked fight with a juvenile male on the first night of the test period. In general, there tended to be more chases on the first night compared to the fourth night (Table 52). Lactating females were observed to chase both juvenile males and juvenile females, but nonlactating females never chased juvenile females. Juvenile males and juvenile females chased nonlactating females and adult males, respectively, but never chased lactating females. Juveniles tended to avoid adults more than adults avoided juveniles (Table 53). Mutual avoidance was not prevalent between juvenile males and nonlactating females. Conclusions, beyond the observation that both aggressive and avoidance behaviors were noted, cannot be firmly made.

Reproduction. Juvenile males and females were involved in pregnancies (Table 54). This indicates that some of the juveniles were sexually mature at a maximum of 44 days of age. Therefore, sexual behavior may be involved in determining the settlement pattern of dispersing juveniles. Since the pregnancies occurred during the four-day period, pair-bonding in P. m. bairdi seems to be a rapid process.

Table 52. The total number of chases per treatment group. Each cell represents 300 15-second intervals.

		First Night			Fourth Night	
		Adult Chased Juvenile	Juvenile Chased Adult		Adult Chased Juvenile	Juvenile Chased Adult
Juvenile Male						
Adult						
Male	(17)	5	0	(11)	1	0
Nonlactating Female	(69)	6	6	(28)	0	0
Lactating Female	(55)*	10	0	(0)	0	0
Juvenile Female						
Adult						
Male	(22)*	0	0	(50)	2	2
Nonlactating Female	(6)*	0	0	(16)	0	0
Lactating Female	(20)	26	0	(55)	0	0

Note: The numbers in parantheses are numbers of 15-second intervals during which mice were observed together in resident area.
* = 292 15-second intervals.

Table 53. The total number of avoidance and mutual avoidance behaviors per treatment group. Each cell represents 300 15-second intervals.

		First Night				Fourth Night		
		Adult Avoided Juvenile	Juvenile Avoided Adult	Mutual Avoidance		Adult Avoided Juvenile	Juvenile Avoided Adult	Mutual Avoidance
<u>Juvenile Male</u>								
<u>Adult</u>								
Male	(17)	0	5	0	(11)	0	8	0
Nonlactating Female	(69)	3	2	30	(28)	0	6	0
Lactating Female	(55)*	0	6	0	(0)	0	0	0
<u>Juvenile Female</u>								
<u>Adult</u>								
Male	(22)*	0	5	0	(50)	3	9	0
Nonlactating Female	(6)*	0	0	2	(16)	1	5	0
Lactating Female	(20)	0	0	0	(55)	0	3	2

Note: The numbers in parantheses are numbers of 15-second intervals during which mice were observed together in resident area.
* = 292 15-second intervals.

Table 54. Treatment group summary of the number of juveniles involved in pregnancies (N = 5).

Experiment	Adult	Juvenile Male	Juvenile Female
Field	Male	-	2
	Female	1	-
Laboratory	Male	-	-*
	Female	1	-

*N = 4 because 1 juvenile was inadvertently sacrificed prior to the end of the three-week post-test period.

DISCUSSION

The general hypothesis of this study was that the outcomes of juvenile-adult interactions in P. m. bairdi would depend upon both juvenile and adult social factors. Interactions between a juvenile male or female and an adult male, a nonlactating female, or a lactating female were studied in field or laboratory enclosures over four-day periods. Juveniles with no adults were used as controls against environmental factors extrinsic to the experiments. The specific working hypotheses were that the sex of juveniles and the sex of adults and/or the reproductive stage of adult females would affect both (1) the settlement of juveniles and (2) the weight change of juveniles. Also, it was expected that the effects of the biological classes would be similar under field-enclosure conditions and laboratory conditions.

The first working hypothesis concerning juvenile settlement was partially confirmed in respect to both juvenile and adult social factors; the effects of social factors varied depending upon the social combinations of interacting animals. Contrary to that expected, the effects of the biological classes on juvenile settlement were not consistent in the field and laboratory experiments. The second working hypothesis concerning juvenile weight change was partially confirmed in respect to juvenile sex, but it was rejected for the adult social factors. As expected, the effects of the biological classes on juvenile weight change were consistent in the field and laboratory experiments.

Juvenile settlement and weight change are discussed separately in reference to: (1) the effects of social factors, (2) the juvenile-adult social relationships, and (3) the consequences for free-ranging _P_. _m_. _bairdi_ populations.

Juvenile Settlement

The importance of juvenile and adult social factors in affecting juvenile settlement in _P_. _m_. _bairdi_ was evaluated experimentally by determining the propensity of juveniles: (1) to nest, during the daytime, in enclosures occupied by adults (nesting location), (2) to share nests with adults, if juveniles nested in enclosures occupied by adults (nesting arrangement), and (3) to remain, during the nighttime active period, in enclosures occupied by adults (time variable). Each of these dependent variables served as a measure of juvenile settlement, and significant differences among social combinations were judged to indicate relative effects of adults in limiting juvenile settlement.

Effects of Social Factors. Nonlactating females limited the settlement of juvenile females compared with juvenile males based upon the significant differences in the nesting arrangement variable during the field experiment and in the mean time variable during the laboratory experiment. Also, in the laboratory experiment, juvenile females tended to nest in resident areas occupied by nonlactating females less frequently than did juvenile males. Differences in juvenile male and female settlement were not significant when adult males or lactating females were encountered. That social interactions, and not a fundamental difference between juvenile sexes, led to differences in juvenile settlement was indicated by the failure to detect significant differences between the male and female juveniles that were placed in the control conditions with no adult.

Differences in juvenile settlement due to the effect of the sex of adults and/or the reproductive stage of adult females were detected for the mean time variable in the laboratory experiment. Lactating females, compared to adult males, nonlactating females, and the control condition with no adult, limited the settlement of juveniles, but this difference was significant for juvenile males only. The analysis of the nesting arrangements for the laboratory experiment indicated that the settlement of both male and female juveniles tended to be limited by lactating females. A similar finding was obtained in the analysis of the nesting arrangements in the field experiment, except that the settlement of juvenile females appeared to be also limited by nonlactating females. The latter two nesting arrangement differences closely approached significance.

Experiments were repeated under two environmental conditions in order to determine if the social variables had the same relative influence in two conditions of space quality. Contrary to that expected, the experimental physical environment was an important factor in determining the outcomes of juvenile-adult interactions in respect to juvenile settlement. Nesting arrangements were significantly different among social combinations in the field experiment, and both the nesting location and the mean variables were significantly different among social combinations in the laboratory experiment.

The confined and sterile space of the laboratory enclosures probably led to an increase in the number of contacts between the interacting prairie deer mice, which, in turn, increased the frequency of the behaviors that resulted in better resolution of the nesting location variable and the mean time variable over that in the field experiment. However, since fewer juveniles nested in the resident area during the laboratory experiment, sample size was decreased to a point where the nesting arrangement measure did not significantly differentiate between the effects of social factors, though borderline significance was obtained. On the other hand, the nesting arrangement measure could be used to detect significant and borderline to significant differences among social combinations in the field experiment. In general, it can be concluded that the laboratory experiment obtained more conclusive evidence for the effects of social factors on juvenile settlement. The point should be made that the validity of the laboratory results was not reduced by the proposed high frequency of behavioral interactions because juveniles could escape the presence of adults by moving to the dispersal areas.

The claim that the frequency of behavioral interactions was dependent upon the enclosure size is in agreement with the findings of Colvin (1973). This investigator found that the frequency of agonistic postures of Microtus males was inversely related to enclosure size. The grassland habitat of the field enclosures in the present experiment may have also served to decrease the frequency of contacts and behavioral interactions and/or increase avoidance by providing cover and refuge sites. The effects of changes in weather conditions are not known.

The four-night means of the time measure were reliable in determining consistent differences among social combinations in the laboratory experiment. Contradictory significant differences were not detected in the analysis of the individual nightly values. The significant differences between juvenile males and females that interacted with nonlactating females were present on all four nights, and significant differences among adult classes for juvenile males were found on the last three nights. These results suggest that the respective social relationships were established at least by the second night and remained stable during the course of the experiment.

Social Relationships. The results of this study on *P. m. bairdi* indicate that nonlactating and lactating females, but not adult males, may limit the settlement of dispersing juveniles depending upon their sex. These findings are contradictory to the conclusions of Sadleir (1965) and Healey (1967), for *P. m. austerus*, and Flowerdew (1974), for *A. sylvaticus*, but are consistent with Metzgar's (1971) findings for *P. leucopus*. However, the effects of different female reproductive stages were not determined in the latter study and the results of the present investigation are more specific. The different conclusions may reflect upon differences in the social behavior of the different taxa and/or upon the failure of previous investigators to consider the biological determinants of social behavior.

Peromyscus maniculatus austerus and *A. sylvaticus* males are aggressive towards juveniles, but nonlactating females typically are not (Healey, 1967, and Flowerdew, 1974). However, in *P. m. bairdi*, lactating females frequently wounded juveniles, but adult males and nonlactating females were typically nonaggressive. Direct observations provided no support of the relative aggressiveness of lactating females, based upon wounding, because the prairie deer mice in the present study infrequently interacted, and conclusive patterns in the relative levels of agonistic behaviors could not be determined. Hill (1970) reported low frequencies of behavioral interaction between adult P. leucopus and P. m. bairdi and suggested that high levels of social interaction may not be necessary to produce significant effects on the spatial relationships of Peromyscus.

The relative limitation of juvenile male settlement by lactating females can be explained by the presence of maternal aggression directed towards strange juveniles. There was some evidence to indicate that lactating females, compared with adult males, also limited the settlement of juvenile females, though the results of the statistical analyses were not conclusive. It may be suggested that immature female P. m. bairdi do not recognize differences among adult social classes as markedly as do young males and therefore do not form different social relationships as readily. On the other hand, lactating females may be less aggressive towards juvenile females than they are towards juvenile males. Although, it is doubtful that differential aggressiveness exists because Savidge (1974) found that, in P. m. bairdi, there is no difference in the dispersal rates of male and female juveniles in response to aggression by their mother. This implies that the adult females were similarly aggressive towards male and female offspring. Also, the possibility exists that the treatment combination sample sizes of the present experiment were not sufficiently large to detect true differences, if they existed.

A functional explanation for the failure of adult males to limit the settlement of juvenile males in the present study is not available. It may be suggested that P. m. bairdi males are more social than previously reported (Howard, 1949), and juveniles do not avoid adults upon encounter. Myton (1974) implied that P. leucopus males are more social than females, and Metzgar (1971) found that resident female P. leucopus appeared to limit the number of transient females that settled in a local population, but males did not limit the settlement of juvenile males. The same relationship may exist in P. m. bairdi even though Hill (1970) observed no difference in the levels of aggression during adult female-female and male-male encounters.

In the present study, nonlactating females limited the settlement of juvenile females compared with juvenile males, but nonlactating females seldom wounded juveniles. It appears that the juvenile females avoided the nonlactating females in the absence of overt aggression. Terman (1962) and Hill (1970) indicated that Peromyscus commonly avoided conspecifics upon encounter, and suggested that animals may be organized in space without aggressive interaction. It should be mentioned that agonistic interaction may involve behavioral patterns that do not include direct fighting (Scott, 1972). These would not be detected by an examination of wounding as was done in the present study.

The differences in settlement between the male and female juveniles that interacted with nonlactating females can also be explained in terms of the establishment of sexual relationships between the young males and the nonlactating females. Sexual relationships were present between juvenile females and adult males as well. Compared with lactating females, the failure of adult males and nonlactating females to limit the settlement of juvenile females and males, respectively, might be expected because home ranges of opposite sexes in Peromyscus usually overlap more than those of individuals of the same sex (see Stickel, 1968) and P. m. bairdi form monogamous pair-bonds (Howard, 1949).

Successful pair-bonds may be formed over a four-day period because both male and female juveniles were involved in pregnancies. That most (about 80%) of the juveniles were not involved in pregnancies during the experiments indicates that individual differences in sexual maturity existed among juveniles because all adults were in breeding condition. Of course, another possible explanation is that pair-bonding and impregnation typically takes longer than four days. Hill (1970) found that nine out of ten _P_. _m_. _bairdi_ adult pairs bred within a seven-day period.

Finally, the relative differences in the laboratory experiment nesting area and per cent time measures were not consistent with the lack of differences in the rate at which juveniles entered and left the resident areas. It appears that the relatively exclusive or nonexclusive use of space by juvenile and adult _P_. _m_. _bairdi_, as determined by social interactions, is not permanent. That is, the degree of mutual use of the resident areas by juveniles and adults was not related to the frequency at which juveniles entered and left the resident areas. This finding is in accordance with the reported influx of neighboring _P_. _leucopus_ into depopulated areas (Stickel, 1946). _Peromyscus_ may be envisioned as constantly probing the periphery of their home ranges, and using new space or establishing new social relationships if the opportunity arises. Hill (1970) reported that _Peromyscus_ use space as it becomes available to them. Yet most individuals in free-ranging populations are arranged spatially in stable home ranges, though some individuals may switch home ranges (see Stickel, 1968). The social behaviors determining the spatial organizations of _Peromyscus_ populations are not apparent, but it is known that _Peromyscus_ is not territorial (Hill, 1970).

Different rodent taxonomic groups have been reported to vary in respect to male and female aggressiveness (Steiner, 1972, and Michener, 1973 for *Spermophilus*, and Eisenberg, 1963 for *Peromyscus*). It is not suggested herein that aggressive males are unimportant in determining the juvenile settlement for some groups because much evidence is available to document the contrary (*e.g.*, Carl, 1971). The point to be made is that generalizations from such groups (*e.g.*, *P. m. austerus*, Healey, 1967) to other taxa (*e.g.*, *P. m. bairdi*) are premature until future comparative studies are conducted. Further, the results of this study show that settlement may be influenced by both juvenile and adult social factors, and social relationships that do not involve aggression may be formed during the settlement process. In summary, the social organizations of small rodents may be characterized by various social relationships that differ among taxa. That these differences may exist between *Peromyscus* subspecies is not surprising because significant differences have been reported in habitat selection (Harris, 1952) and several other behavioral responses including activity (Foster, 1959) for *P. maniculatus* subspecies. Correlates of the potentially different social organizations such as modes of environmental exploitation, habitats, and life histories present intriguing topics of future comparative research. These investigations should add insight into the functional significance of the various social systems. The role of lactating females should not be overlooked in such studies because maternal aggression may be an important general phenomenon in *Peromyscus* and other rodents.

Consequences of Juvenile-Adult Interaction. The results of the present study allow some inferences to be made concerning the consequences of juvenile-adult interactions on juvenile settlement in P. m. bairdi, if the social relationships in free-ranging populations are similar to those found using enclosures. The population biology information has been taken from Howard's (1949) report. It has been assumed herein that the sex ratio of dispersing juveniles is constant over time, although there may be a larger number of males than females born into a population as was found by Terman and Sassaman (1967) for a laboratory colony of P. m. bairdi. Only intraspecific social interactions have been considered, but interaction with other rodent species (Grant, 1972) and availability of physical environment requirements such as nest sites (Rose and Gains, 1976) may influence settlement in rodents.

Dispersal and subsequent settlement occurs during the breeding season (warmer months) in P. m. bairdi. During periods of peak reproduction (spring and late summer-fall) when a high percentage of the resident females are nursing young and exhibiting maternal aggression, juvenile males should be less likely to settle than at other times when reproduction within the population is lower (mid-summer). Since young females appear to be similarly limited by nonlactating and lactating females, the ratio of juvenile males-to-females that successfully settle should vary directly with the ratio of nonlactating-to-lactating females in the population. There is some indication that the settlement of juvenile females is limited by adult females, but there is no indication that adult males limit the settlement of juvenile males. To summarize, the settlement of young males is suggested to be related to the reproductive activity of adult females within the population, whereas the settlement of immature females may be related to the population density of resident females.

It is noteworthy to mention some relationships between the proportion of P. maniculatus females in local populations and population densities as determined by Terman and Sassaman (1967) from analyses of NACSM data. These data were obtained from local populations in successive seasons (spring-fall-spring) or the same season through successive years (spring-spring, fall-fall). In the successive seasons and spring-spring comparisons, the proportion of females increased or decreased when population densities were increasing or decreasing, respectively, significantly more frequently than when population densities were decreasing or increasing, respectively. A similar pattern existed for the fall-fall comparisons, but it was not significant. This relationship between the proportion of females in the population and the population density changes may indicate that the ratio of juvenile males-to-females that settled into the populations varied directly with the ratio of nonlactating-to-lactating females. Though it was not mentioned if changes in the population densities were related to changes in reproductive activity within the populations. The same comparisons for P. leucopus populations were nonsignificant.

Three points should be mentioned with the proposed settlement model in mind. Firstly, since reproductive activity in P. m. bairdi and other Peromyscus species (e.g., Rintamaa, et al., 1976) decreases during mid-summer for unknown reasons, the increased settlement of males would probably not be due to sexual relationships being formed with nonlactating females. The causative factor would more likely be a decrease in the percentage of resident females that are lactating.

Of course, if young males settle near nonlactating females, then the chances are great that they would be involved in reproduction during the fall breeding peak. The second point is that the assumption that juveniles disperse only as far as is required to reach a suitable settlement site is implicit in this verbal model. It follows that dispersal distance for males would vary in response to changes in the ratio of nonlactating-to-lactating females. However, several field studies on Peromyscus have obtained evidence for slightly greater dispersal distances in males (see Stickel, 1968, and Howard, 1949 for P. m. bairdi), though these studies did not attempt to relate dispersal distance with the population reproductive activity. The reasons for the differing dispersal distances are not known, but these may be related to differences in activity or trapability (Terman, 1968). The third and final point is that while P. m. bairdi has been reported to form monogamous pair-bonds (Howard, 1949), the present research evaluated social interaction between two animals only to obtain specific information. The behavior of adult males toward juveniles may depend upon the presence of an adult female. Still, the mechanisms associated with pair-bonding are not known. The fact that Birdsall and Nash (1973) reported that some P. maniculatus litters (11 of 107 examined) contained at least three different alleles of parental origin indicates that the monogamous pairs are not consistently maintained.

The proposed settlement model can be explained on the basis of individual selection. If an individual remained in the presence of hostile social conditions and/or where the chances of successful reproduction were low, the fitness of that individual would be correspondingly low. Therefore, juveniles should continue to disperse in order to increase the probability of reproductive success as long as the potential gain of moving is greater than the potential cost of remaining in an area. Murray (1967) gave a similar and more detailed argument, but did not consider the role of social relationships other than dominance-subordinance. Healey (1967) discussed the individual selective advantages of aggressiveness in _P_. _m_. _austerus_ adult males in respect to their role in affecting the settlement and survival of immigrating juvenile conspecifics. These proposed advantages are consistent with Murray's suggestions.

The evolutionary significance of the proposed relationships in _P_. _m_. _bairdi_ between the population reproductive activity and the settlement of juvenile males and the population density of resident females and the settlement of juvenile females is not clear. However, these proposed correlates may be due to the selection for different social relationships that consequently effect population regulation, though the present study was not designed to evaluate mechanisms of population regulation and future research is required.

The numbers of young _P_. _m_. _bairdi_ produced are in excess of the numbers that settle within a population. Local populations should be limited at an absolute density that can be supported by the area with the surplus juveniles dispersing into neighboring populations or being taken by predators. It can be speculated that the ultimate determinant of population density in _P_. _m_. _bairdi_ is the number of resident, breeding females within a population. If the number of adult females is limited at some maximum level, the absolute production of young will also be limited. However, the production of young per female will be maximized at a level that can be supported by the resources in the natal home ranges. The survival of offspring will be enhanced if lactating females repulse strange juveniles that would be competitors for the available resources in the natal home ranges. Nonlactating females might be expected to repulse juvenile females because a single home range may not provide adequate resources for two lactating females and their litters in the event that adults and juveniles become pregnant. On the other hand, nonlactating females should not repulse juvenile males because of the potential for future breeding. Whether males compete for available home ranges and mates, as is the case in other rodents (_e_._g_., Carl, 1971), awaits future study.

It should be noted that mother-offspring interactions may be influenced by different selection pressures than those between strange animals because the mother and offspring are related by one-half. Offspring might be repulsed in order to reduce the chances of parent-offspring matings, especially if the parental males remains near the natal site. However, Williams (1976) suggested that, under certain conditions, inbreeding may be adaptive. Also, the inclusive fitness of the mother may be increased if she permits her offspring to establish breeding home ranges near the natal site because the risk incurred to the offspring while traveling across unfamiliar terrain would be reduced. Alternatively, the inclusive fitness of the mother might be reduced if offspring breed nearby because the natal area may not contain sufficient resources to support several lactating females and their litters. Savidge (1974) reported that adult _P_. _m_. _bairdi_ females differ in aggressiveness and in the consequent repulsion of offspring. However, whether differences exist in the behavior of adult females towards offspring and strange juveniles has not been determined and should be the topic of future research.

Dispersal may affect the densities, age and social structures, and sex ratios of local populations (Lidicker, 1975). Advances in the understanding of the population biology of small mammals can be made by studying the three phases of dispersal independently. Eventually, the attainment of a complete understanding of dispersal will require that investigations be conducted on the abiotic and biotic factors that influence all three phases (leaving the natal area, crossing unfamiliar space, and settlement) in field populations. Then this understanding can be integrated into the study of mortality and natality at the population level. At present, studies such as these, as well as an evaluation of the proposed settlement model for *P. m. bairdi*, are not feasible because adequate sampling technologies are not available.

The results of this study suggest two lines of research that could be conducted using enclosures to provide adequate control over experimental animals. Firstly, the preference of juveniles for adults should be examined. This study would be especially helpful in giving greater resolution in the juvenile male-adult male and the juvenile male-non-lactating female relationships. Secondly, and of more immediate interest, the effect of adult pairs on juvenile settlement should be evaluated. If adult females, and not adult males, limit the settlement of dispersing juveniles, then the presence of an adult male along with an adult female should not influence the response of juveniles toward adults and *vice versa*. This study would conclusively determine (1) whether adult females limit the settlement of juveniles and (2) whether juvenile-adult male social relationships are dependent upon the presence of an adult female. Taken together, the results of these two tests would challenge the existence of the social relationships necessary for the proposed settlement model.

Juvenile Weight Change

The importance of juvenile and adult social factors in affecting the growth of juvenile *P. m. bairdi* was evaluated by examining the difference between initial and final weights of juveniles. Both the sex of juveniles and the sex of adults and/or the reproductive stage of adult females were hypothesized to affect juvenile growth. It was expected that the effects of the biological classes would be similar under field-enclosure conditions and laboratory conditions.

Effects of Social Factors. A significant difference in juvenile growth rates due to the sex of juveniles was detected for those juveniles that interacted with adult males. In this case juvenile females had lower growth rates than juvenile males. Differences between the male and female juveniles that interacted with nonlactating females or lactating females or encountered the control condition were nonsignificant. There were no significant differences in the growth rates of male or female juveniles among the adult classes, but control juvenile males gained less weight than did those males that interacted with adult males. The weight gain of control juvenile females was similar to that of the females that interacted with the respective adult classes. Juveniles gained significantly more weight during the field experiment compared to the laboratory experiment. However, there were no statistical interactions between the effects of location and either the effects of juvenile or adult social factors. Therefore, it can be concluded that the effects of the social factors on juvenile growth were similar in both experiments.

Social Relationships. The results of the present study on P. m. bairdi do not indicate that adult males inhibit the growth of juveniles compared to nonlactating females or lactating females, although social interaction with adult males caused a difference in the weight gain of juvenile males and females. This conclusion is contradictory to that of Healey (1967) for P. m. austerus; several possible reasons exist for the difference in results. Firstly, Healey allowed adults to interact with juveniles over a 14-day period and social interaction in the present study was limited to four days. Clearly, the longer time period may have been important in increasing the relative differences in weight gain among treatment combinations. But a longer period probably was not necessary to produce significant differences because Healey noted a dramatic weight loss within four days in juveniles released onto field plots containing aggressive males, compared to juveniles released onto field plots containing docile males. The weight loss over the remaining ten days was relatively slight. Secondly, the experimental design used by Healey called for juveniles either to be confined with adults in comparatively small laboratory mazes or to be free to emigrate (disappear) from field plots and be unavailable for the analysis of weight changes. All juveniles in the present study were allowed to avoid adults by entering the dispersal area, however, these animals were included in the analysis. It is not known how this design feature influenced the results of the present study. However, since juvenile settlement was not limited by adult males, compared to nonlactating females or lactating females in both the field and laboratory experiments, it appears that juveniles remained in the presence of adult males. This latter point lends support to the third explanation of the contradictory conclusions. No attempt was made to modify aggression among males in the present study. This difference in designs probably is not important in explaining the difference in results because Healey reported that _P_. _m_. _austerus_ males, irrespective of their aggressiveness, tended to inhibit juvenile growth to a greater degree than did adult females. The differences between results may reflect basic differences in the social behavior of _P_. _m_. _austerus_ and _P_. _m_. _bairdi_ with the former subspecies being more aggressive.

The difference between the weight gain of juvenile males and females that interacted with adult males apparently was not related to aggressive behavior because, as previously mentioned, adult males never wounded juveniles and the direct observations of encounters indicated that adult males behaved similarly towards juvenile males and females. Perhaps the sexual relationship between adult males and juvenile females caused increased activity or decreased food intake and led to the relative retardation of growth. The fact that juvenile males tended to have lower growth rates, compared with juvenile females, when nonlactating females were encountered is consistent with the notion of short-term effects of sexual behavior on the growth rates of juveniles. That the activity rates in the passage tunnel were not different between the juvenile males and females that encountered adult males or nonlactating females indicates that food intake, and not activity, was affected by social interaction. Still, the possibility remains that activity, other than the one measured, could have changed.

Consequences of Juvenile-Adult Interactions. The basic thesis of Healey's study was that aggressive adult males decreased juvenile survival and growth and effected population regulation in *P*. *m*. *austerus*. The inhibition of juvenile maturation resulting from interaction with adults is of great potential importance in determining the status of *Peromyscus* populations, if a decrease in growth rate is related to an increase in the age at which juveniles become sexually mature. Other field investigations are lacking, and data from laboratory studies do not provide conclusive support of either the existence of inhibition or the specific social correlates of inhibition that can be extrapolated to free-ranging *P*. *m*. *bairdi* populations (Terman and Gardner, 1970, and Thomas and Terman, 1975).

Several inferences can be drawn in reference to the effects of social interaction on juvenile growth rates in *P*. *m*. *bairdi* as a result of this study. Firstly, since the abiotic environment of the experiment proved to be a significant factor in affecting the juvenile weight changes, growth measures may be partly spurious to social factors. Additional support of this conclusion is the finding that there were no statistical interactions between the location of the experiments and the social factors, which indicates that these two treatments operated independently of one another. Secondly, failure to detect differences among juveniles that interacted with the respective adult social classes may have been due to the juveniles avoiding the adults within the resident area or moving to the dispersal area. In either case, it is likely that juveniles in free-ranging populations escape potentially adverse social conditions that could cause an inhibition of growth. This conclusion is supported by the finding that interaction with lactating females, the most aggressive adult class, did not cause an inhibition of juvenile growth compared to interaction with the typically nonaggressive adult males or nonlactating females. Therefore, the third inference is that a relative retardation of growth due to short-term social interaction need not be correlated with aggressive behavior. The difference between juvenile males and females that interacted with adult males suggests that sexual relationships may be important in affecting juvenile growth. Fourthly, the differences between juvenile males that encountered adult males or the control condition indicates that social interaction between male *P. m. bairdi* promotes growth compared to situations where interaction is not possible. Perhaps social facilitation influences the food intake or juveniles. This point reflects upon another aspect of the apparent basic differences in the social behavior of *P. m. austerus* and *P. m. bairdi*, and agrees well with the finding that adult males do not limit the settlement of juvenile males.

Future research should be conducted in an attempt to document the occurrence of maturation inhibition under experimental conditions where juveniles can avoid the presence of adults. A study on an aggressive *Peromyscus* taxon, such as *P. m. austerus*, would provide conclusive evidence of whether juveniles avoid hostile social conditions and thereby avoid possible retardation of growth. Another study should examine the role of sexual relationships in affecting juvenile growth. Special attention in both studies should be given to a determination of the immediate mechanisms responsible for differences in juvenile growth rates. Activity and food intake may be the most useful dependent variables in short-term experiments.

Summary

1. Juvenile-adult social interactions in P. m. bairdi were studied using field (3.8 m^2) or laboratory (1.2 m^2) enclosures. The working hypotheses were that the sex of juveniles and the sex of adults and/or the reproductive stage of adult females would affect: (1) the settlement of juveniles and (2) the growth rate of juveniles. It was expected that the effects of the biological classes would be similar under field-enclosure conditions and laboratory conditions.

2. Following a three-day pretest period during which all prairie deer mice could become familiar with the experimental environments, juveniles could become familiar with the test apparatus, and adults could establish residency, a juvenile male or female was placed in an enclosure containing: (1) an adult male, (2) a nonlactating adult female, (3) a lactating female, or (4) no adult as a control. Five replications of each of the eight social combinations were used in the field and laboratory experiments. The juveniles were free to interact with the adults over four-day periods. During the experiments, juveniles could move through a two-way tunnel to an adjacent unoccupied enclosure, but adults could not, and all mice had access to nest boxes.

3. Juvenile settlement was evaluated experimentally by determining the propensity of juveniles: (1) to nest, during the daytime, in enclosures occupied by adults, (2) to nest with adults, if juveniles nested in enclosures occupied by adults, and (3) to remain, during the nighttime active period, in enclosures occupied by adults. Significant differences among social combinations were judged to indicate a relative limitation of settlement. The growth of juveniles was examined by analyzing the difference between their initial and final weights.

Juvenile activity between enclosures, juvenile wounding, and reproductive activity were measured, and direct observations of interactions in the laboratory were conducted.

4. The settlement of juvenile females compared with the settlement of juvenile males was limited by nonlactating females. Differences in settlement due to the sex of juveniles were not significant when juveniles interacted with adult males or lactating females or encountered the control condition of no adult. The effects of adult social factors were significant for juvenile males; lactating females, compared with adult males, nonlactating females, or the control condition, limited the settlement of immature males. However, differences in settlement due to the adult social factors were only borderline to significance for juvenile females; both nonlactating and lactating females, compared with adult males, tended to limit the settlement of immature females. Similar outcomes of social interactions in free-ranging populations would result in nonlactating and lactating females, but not adult males, limiting the settlement of dispersing juveniles depending upon their sex. The effects of the social factors were not consistent in the field and laboratory experiments possibly due to differences in the frequencies of behavioral interaction and/or avoidance.

5. It was proposed that contradictions in the results of previous studies on Peromyscus (e.g., Healey, 1967) and the present research are due to differences in social behavior of the different taxa and/or the failure of past workers to consider the biological determinants of social behavior. Lactating P. m. bairdi frequently wounded juveniles, but adult males and nonlactating females were typically nonaggressive towards juveniles. Also, sexual relationships were formed between

adults and juveniles because some juveniles were involved in pregnancies during the experiments.

6. The relative differences in the laboratory experiment nesting area and per cent time measures were not consistent with the lack of differences in the rate at which juveniles entered and left the resident areas. That is, the degree of mutual use of the resident areas by juveniles and adults, as determined by social interactions, was not related to the frequency at which juveniles entered and left the resident areas. This is in agreement with previous reports on the utilization of available space in Peromyscus.

7. Juvenile females, compared with juvenile males, had significantly lower growth rates when adult males were encountered. Differences in growth rates between male and female juveniles that interacted with nonlactating females or lactating females, and differences between control juveniles, were nonsignificant. There were no significant differences in the growth rates of male or female juveniles due to the adult social factors, but control juvenile males gained significantly less weight than did those males that interacted with adult males.

8. These results may also reflect differences in the social behavior of different Peromyscus taxa. However, behaviors other than aggression, such as sexual behavior, may affect juvenile growth by altering juvenile activity and/or food intake. The effects of the social factors on juvenile growth rates were similar under the two conditions of space quality. But juveniles in the field experiment gained significantly more weight than the juveniles in the laboratory experiment. Therefore, differences in juvenile growth rates may be partly spurious to social factors, at least on a short-term basis.

APPENDIX A

APPENDIX A

ANALYSIS OF THE DISAPPEARANCE OF JUVENILES DURING THE FIELD EXPERIMENT

No adults were lost from the field enclosures, but several juveniles escaped or were taken by predators. A 2-way contingency table showed that the proportions of juvenile males and females that disappeared from these enclosures were close to being significantly different ($P \approx .06$, Table 74). The data from the field experiment were evaluated under the assumption of equal disappearance of juvenile males and females. However, only data collected from juveniles that completed the experiment were analyzed.

Table 74. Chi square analysis of the disappearance of juveniles during the field experiment.

	Juvenile Male	Juvenile Female
Disappeared	9	2
Did not disappear	20	20

$\chi^2 = 3.5608$, df = 1, $P \approx .06$

APPENDIX B

APPENDIX B

JUVENILE ACTIVITY WITHIN AREAS

The activity of juveniles within the resident and dispersal areas, expressed as the number of feeder tunnel trips per hour juveniles had access to feeders during the active period, was examined to determine if the experimental social conditions influenced the movement of juveniles within areas. The proportion of juveniles that tripped feeder tunnels in the field experiment was significantly smaller than that in the laboratory experiment ($.005 > P$, Table 55 for the resident area and Table 56 for the dispersal area).

The four-night mean activity rates within the resident and dispersal areas are given in Table 57; these data were analyzed with nonparametric statistics (Tables 58 and 59, respectively). No significant differences were found for the main effects of juvenile sex or adult class. The juvenile sex x adult class interaction was nonsignificant as well. The results for the field experiment indicate that social conditions did not affect the juvenile activity rate in either the resident or dispersal areas.

The back transformed within area activity rate means obtained in the laboratory experiment are given in Table 60. These data were examined by analyses of variance after the raw scores for each replication were transformed to the $\sqrt{y + 1/2}$ scale. The tables and figures showing the differences among means give the transformed values.

Neither the juvenile sex nor adult class main effects were significant for the resident area activity, but there was a significant

Table 55. Chi square analysis of the proportions of juveniles that tripped the feeder tunnels in the resident area during the field and laboratory experiments.

	Tripped Tunnels	Did Not Trip Tunnels
Field Experiment	9	31
Laboratory Experiment	29	11

$\chi^2 = 20.0501$, df = 1, .005 > P

Table 56. Chi square analysis of the proportions of juveniles that tripped the feeder tunnels in the dispersal area during the field and laboratory experiments.

	Tripped Tunnels	Did Not Trip Tunnels
Field Experiment	9	31
Laboratory Experiment	32	8

$\chi^2 = 26.4665$, df = 1, .005 > P

Table 57. The four-night group means of the number of feeder tunnel trips per hour of the active period during the field experiment (N = 5).

	Juvenile Male				Juvenile Female			
Adult:	Male	Nonlactating Female	Lactating Female	Control (No Adult)	Male	Nonlactating Female	Lactating Female	Control (No Adult)
				Resident Area				
Four-night $\bar{x}$	0.03 (1)[a]	0.40 (2)	0.59 (2)	0.00 (0)	0.20* (1)	0.36 (1)	0.00 (0)	0.14 (1)
				Dispersal Area				
Four-night $\bar{x}$	0.41 (1)	1.25 (2)	0.40 (1)	0.00 (0)	0.20 (1)*	0.24 (2)	0.00 (0)	0.36 (1)

*N = 4 due to equipment malfunction.
a = number of juveniles that tripped the feeder tunnels.

Table 58. Nonparametric analysis of the four-night mean juvenile activity rate in the resident area during the field experiment.

Comparison	Test	W_n or H/D Value	Prob.
Juvenile	Wilcoxin's rank-sum test	$W_n = 26$	$P > .1$
Adult	Kruskal-Wallis test	H/D = 0.8261	$.9 > P > .5$
Juvenile x Adult Interaction	Kruskal-Wallis test	H/D = 4.9912	$.5 > P > .1$

Table 59. Nonparametric analysis of the four-night mean juvenile activity rate in the dispersal area during the field experiment.

Comparison	Test	W_n or H/D Value	Prob.
Juvenile	Wilcoxin's rank-sum test	$W_n = 27$	$P > .1$
Adult	Kruskal-Wallis test	H/D = 1.7387	$.9 > P > .5$
Juvenile x Adult Interaction	Kruskal-Wallis test	H/D = 1.8602	$.9 > P > .5$

Table 60. The back transformed four-night group means of the number of feeder tunnel trips per hour of the active period during the laboratory experiment (N = 5).

	Juvenile Male				Juvenile Female			
Adult:	Male	Nonlactating Female	Lactating Female	Control (No Adult)	Male	Nonlactating Female	Lactating Female	Control (No Adult)
				Resident Area				
Four-night $\bar{x}$	1.91[a] (0.00-5.66)	0.16 (0.00-0.57)	0.42 (0.00-1.44)	1.11 (0.09-2.64	0.96 (0.41-1.63)	2.71 (0.00-8.40)	2.19 (0.42-4.88)	1.12 (0.00-3.13)
				Dispersal Area				
Four-night $\bar{x}$	1.63 (0.19-3.86	2.86 (0.00-11.52)	0.75 (0.00-2.11)	1.62 (0.24-3.73)	3.08 (1.06-5.92)	3.26 (0.00-10.69)	1.24 (0.14-2.88)	1.81 (0.78-3.14)

[a] = back transformed mean (95% C.L.).

juvenile sex x adult class interaction (.05 > P > .025, Table 61). Analysis of the simple main effects revealed that the sex of juveniles affected their activity within the resident area only when nonlactating females were encountered (.01 > P > .005, Table 61). Figure 18 shows that, in the presence of nonlactating females, juvenile females had a higher activity rate than did juvenile males. None of the other juvenile sex comparisons were significant. But at a borderline significance level, juvenile females, compared with juvenile males, had a higher activity rate when lactating females were encountered (Table 61). The back transformed means for this comparison are shown in Table 60. There were no significant differences among the adult classes for either juvenile males or females. Finally, there were no significant F-values for the juvenile activity rates within the dispersal area (Table 62).

In conclusion, juvenile activity within the resident area was influenced by social factors only in the comparison of juvenile sexes for nonlactating females during the laboratory experiment. Juvenile activity within the dispersal area (in the absence of adults) was affected by neither the juvenile nor adult social factors during the field and the laboratory experiments.

As noted earlier (see Methods), activity measured in a feeder tunnel is subject to confounding variables and might not provide a true estimate of the effects of social factors on locomotor activity. However, the propensity of juvenile rodents to enter and leave feeder tunnels may be related to the inclination to enter live-traps because the same confounding variables are present in both situations. That is, bait preference of individuals and their response to the physical

Table 61. Analysis of variance for the four-night mean juvenile activity rate in the resident area during the laboratory experiment.

Source of Variation	df	MSS	F-value	Prob.
Juvenile	1	1.0365	3.6036	.1 > P > .05
Adult	3	0.0234	0.0813	.9 > P > .5
Juvenile x Adult	3	0.8901	3.0945	.05 > P > .025
Error	32	0.2876		
Total	39 (SS = 12.9812)			
Simple Main Effects of Juvenile For:				
Adult Male	1	0.2958	1.0284	.5 > P > .25
Nonlactating Female	1	2.2563	7.8445	.01 > P > .005
Lactating Female	1	1.1560	4.0191	.1 > P > .05*
No Adult	1	0.0000	0.0000	P > .75
Simple Main Effects of Adult For:				
Juvenile Male	3	0.5429	1.8874	.25 > P > .1
Juvenile Female	3	0.3699	1.2861	.5 > P > .25
Error	32	0.2876		

*Indicates borderline significance where the calculated value was within .20 units of the critical value.

Figure 18. Graph showing the significant difference (.01 > P > .005) in the four-night mean juvenile male and female activity rate in the resident area occupied by nonlactating females in the laboratory experiment. The vertical lines indicate ± 1 S.E. (N = 5).

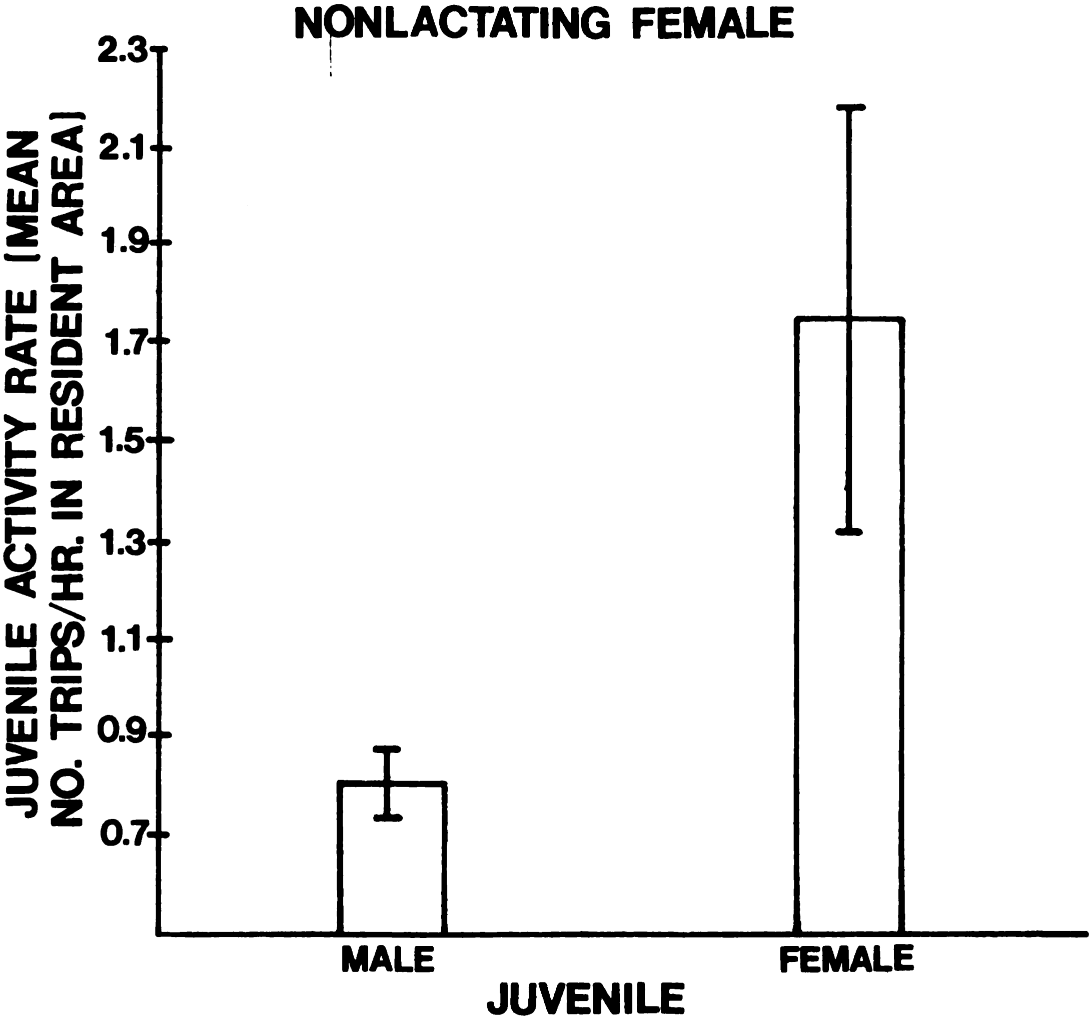
NONLACTATING FEMALE
JUVENILE ACTIVITY RATE (MEAN NO. TRIPS/HR. IN RESIDENT AREA)
2.3
2.1
1.9
1.7
1.5
1.3
1.1
0.9
0.7
MALE
FEMALE
JUVENILE

Figure 18.

Table 62. Analysis of variance for the four-night mean juvenile activity rate in the dispersal area during the laboratory experiment.

Source of Variation	df	MSS	F-value	Prob.
Juvenile	1	0.4016	0.7631	.5 > P > .25
Adult	3	0.8023	1.5244	.25 > P > .1
Juvenile x Adult Interaction	3	0.0680	0.1292	P > .75
Error	32	0.5263		
Total	39 (SS = 19.8534)			

aspects of the feeder or trap may influence movement into these structures. The findings of the present study are in conflict with suggestions that adult small rodents decrease the trapability of juveniles by somehow restricting juvenile movement (Watts, 1970). These data will be presented in a future paper.

APPENDIX C

APPENDIX C

ANALYSES OF THE DAILY NESTING AREA FREQUENCIES

Table 63. Chi square analyses of the daily nesting area frequencies. These comparisons show the lack of joint independence of location of the experiment, juvenile sex, and adult class.

	df	χ^2-value	Prob.
Day 1	3	29.1976	$.005 > P$
Day 2	3	33.4616	$.005 > P$
Day 3	3	34.2857	$.005 > P$
Day 4	3	29.8039	$.005 > P$

Table 64. Chi square analyses of the daily nesting area frequencies of juveniles for the eight treatment combinations used in the field experiment.

	df	χ^2-value	Prob.
Day 1	3	4.4444	$.5 > P > .1$
Day 2	3	4.0306	$.5 > P > .1$
Day 3	3	8.6275	$.025 > P > .01$
Day 4	3	5.0000	$.5 > P > .1$

Table 65. Chi square analyses of the daily nesting area frequencies of male and female juveniles during the field experiment. The data were pooled for the adult classes.

	df	χ^2-value	Prob.
Day 1	1	0.0000	$.975 = P$
Day 2	1	0.2423	$.9 > P > .5$
Day 3	1	0.7843	$.5 > P > .1$
Day 4	1	0.1732	$.9 > P > .5$

Table 66. Chi square analyses of the daily nesting area frequencies of juveniles during the field experiment. The data were pooled for the juvenile sexes to examine differences among the adult classes.

	df	χ^2-value	Prob.
Day 1	3	1.1310	$.9 > P > .5$
Day 2	3	1.9558	$.9 > P > .5$
Day 3	3	3.9200	$.5 > P > .1$
Day 4	3	2.5000	$.5 > P > .1$

Table 67. Chi square analyses of the daily nesting area frequencies of juveniles for the eight treatment combinations used in the laboratory experiment.

	df	χ^2-value	Prob.
Day 1	3	14.4000	$.005 > P$
Day 2	3	22.9333	$.005 > P$
Day 3	3	17.3737	$.005 > P$
Day 4	3	15.9399	$.005 > P$

Table 68. Chi square analyses of the daily nesting area frequencies of juvenile males and females for adult males during the laboratory experiment.

	df	χ^2-value	Prob.
Day 1	1	1.1110	$.5 > P > .1$
Day 2	1	1.1110	$.5 > P > .1$
Day 3	1	2.5000	$.5 > P > .1$
Day 4	1	2.5000	$.5 > P > .1$

Table 69. Chi square analyses of the daily nesting area frequencies of juvenile males and females for nonlactating females during the laboratory experiment.

	df	χ^2-value	Prob.
Day 1	1	4.2860	$.05 > P > .025$
Day 2	1	4.2860	$.05 > P > .025$
Day 3	1	4.2860	$.05 > P > .025$
Day 4	1	1.6666	$.5 > P > .1$

Table 70. Chi square analyses of the daily nesting area frequencies of juvenile males and females for lactating females during the laboratory experiment.

	df	χ^2-value	Prob.
Day 1	1	0.4760	$P \simeq .5$
Day 2	1	1.1111	$.5 > P > .1$
Day 3	1	1.1111	$.5 > P > .1$
Day 4	1	0.0000	$.975 = P$

Table 71. Chi square analyses of the daily nesting area frequencies of juvenile males and females for the controls with no adult during the laboratory experiment.

	df	χ^2-value	Prob.
Day 1	1	1.6666	$.5 > P > .1$
Day 2	1	2.5000	$.5 > P > .1$
Day 3	1	0.0000	$P = .975$
Day 4	1	4.2850	$.05 > P > .025$

Table 72. Chi square analyses of the daily nesting area frequencies of juvenile males during the laboratory experiment.

	df	χ^2-value	Prob.
Day 1	3	11.4670	$.01 > P > .005$
Day 2	3	19.9990	$.005 > P$
Day 3	3	14.7250	$.005 > P$
Day 4	3	7.6920	$.1 > P > .05$

Table 73. Chi square analyses of the daily nesting area frequencies of juvenile females during the laboratory experiment.

	df	χ^2-value	Prob.
Day 1	3	2.4000	$.5 > P > .1$
Day 2	3	4.0000	$.5 > P > .1$
Day 3	3	2.2222	$.9 > P > .5$
Day 4	3	4.7619	$.5 > P > .1$

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