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dissertation entitled

DISPERSAL IN SEMI-NATURAL POPULATIONS OF PEROMYSCUS MANICULATUS: SEASONAL AND HORMONAL RELATIONSHIPS

presented by

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has been accepted towards fulfillment
of the requirements for

Ph.D. degree in Zoology

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Date November 11, 1983

DISPERSAL IN SEMI-NATURAL POPULATIONS OF *PEROMYSCUS MANICULATUS*: SEASONAL AND HORMONAL RELATIONSHIPS

By

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A DISSERTATION

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

DOCTOR OF PHILOSOPHY

Department of Zoology

1983

ABSTRACT

DISPERSAL IN SEMI-NATURAL POPULATIONS OF PEROMYSCUS MANICULATUS: SEASONAL AND HORMONAL RELATIONSHIPS

By

Kevin Labran Murphy

In prairie deermice (Peromyscus maniculatus bairdi), juvenile dispersers are often pubertal. Furthermore, the rate of departure from the natal area by young P. m. bairdi is usually greatest during the spring and summer, a period which coincides with the season of greatest reproductive recruitment of juveniles into the population.

Causes for this post-natal dispersal may vary, and several hypotheses that address these in small mammals were reviewed. One hypothesis, the sexual search hypothesis, predicts that the: 1) departure rate of juveniles from their natal area will be positively associated with levels of sexually attractive stimuli present in the environment, 2) pubertal mice will be more likely to disperse than non-pubertal individuals, and 3) age at dispersal by juveniles can be experimentally delayed by suppressing their sexual maturation, or advanced by sexual stimulation. These predictions were tested in a series of controlled field experiments with P. m. bairdi in south-central Michigan.

Populations of known familial composition were established by introducing mated pairs of deermice into an old-field artificially

provided with favorable microhabitats. These microhabitats consisted of mouse-accessible enclosures with nest-boxes, surplus food, and water. This semi-natural arrangement provided at least partial control of variables (e.g. population density, predation pressure, nutrition, and intraspecific competition) which are suspected to be causally related to dispersal.

Juveniles were experimentally treated with melatonin implants in one experiment to delay gonadal maturation; while, in another experiment, they were treated with gonadal steroids in an attempt to stimulate sexual activity.

Positive seasonal and hormonal relationships between age at puberty and age at dispersal were found. The results indicated that: 1) pubertal mice were more likely to disperse than non-pubertal individuals, 2) age at puberty was a good predictor of age at disappearance for all mice from all seasons, 3) summer-born, and melatonin-treated mice attained puberty and dispersed at an older age than their spring and control counterparts, 4) in the fall, dispersal rates of steroid-treated mice did not differ from controls.

The close association between age at post-natal dispersal and ontogenetic maturation of the gonads lends credence to the argument that gonadal hormones may be important in activating mate-seeking behaviors in mice.

To my parents,
Bernard and Madelene Hulmes Murphy
who made it all possible

ACKNOWLEDGEMENTS

I extend my sincerest thanks to John A. King, my advisor, for his guidance and enthusiastic support throughout this study. I am also grateful to Richard W. Hill, Lawrence I. O'Kelly, and Donald O. Straney for their constructive comments and encouragement. Dr. Straney generously provided computing facilities and programming assistance in the preliminary stages of data analysis. I also thank John L. Gill and Clyde R. Anderson for their assistance with statistical analyses. I thank Susan Hill for providing facilities and materials for the histological analyses.

My special thanks go to the following students who provided dedicated and unselfish assistance in collecting data during the field work: Lori Aldrich, Susan Comeau, Jerry Gidner, Karen Kolbasa, Jay Kralik, Dana Lindemann, and Peggy Vogt.

To my fellow graduate students and friends who provided encouragement and support, I acknowledge my sincerest appreciation.

This research was supported in part by a U.S. Public Health Service Research Grant, 5 R01 MH 29414, and by a teaching assistantship provided by the Department of Zoology.

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INTRODUCTION

Dispersal can be viewed as the movements made by an animal as it departs its natal area (Gaines and McClenaghan, 1980, after Endler, 1977). These movements are "continual rather than periodic" and may occur "within or between generations." This rather simple and general definition belies the difficulty of studying dispersal, a life-history characteristic that is, perhaps, fundamental to all animals (Howard, 1960). The study of these movements in natural populations is particularly difficult for secretive, nocturnal small mammals because dispersal cannot be observed directly. Instead, dispersal movements are monitored indirectly with the aid of live-trapping, nest-boxes, radiotelemetry, and other tracking techniques.

Some general demographic attributes of rodent dispersers are gradually emerging from field studies. For most species studied, dispersal is a density-independent phenomenon. Dispersers are commonly young, lightweight individuals of either sex who move or disappear from their natal area at, or near, the age of puberty (e.g. Bekoff, 1977) though older individuals of certain species also make dispersal movements (see Tardif, 1979). For a more thorough review of the attributes of dispersers, including behavioral and genetic characteristics, see the Literature Review.

Despite knowledge of certain demographic, behavioral, and genetic attributes of dispersers, little is known about the underlying causes

or mechanisms that prompt dispersal in small mammals. In population studies of the cricetine rodent Peromyscus, the season of active breeding is often characterized by an increase in the number of dispersing juveniles which are often pubertal (e.g. Healey, 1967; King, 1983; Saldier, 1965). The coincidence of juvenile dispersal, juvenile sexual maturation, and breeding by resident adults has led to the hypothesis that juveniles move in response to social pressure or aggression from resident males (Gaines and McClenaghan, 1980; Krebs, 1978). Nevertheless, the evidence for the occurrence of social pressure or aggression in natural populations is weak and is derived mainly from questionable laboratory tests or from the assessment of skin wounds. Despite the inferences of aggression in populations, aggressive behaviors of small, nocturnal mammals have rarely been observed in the field (e.g. Anderson, 1980).

Since dispersal occurs predominantly during the breeding season, an alternative explanation for dispersal is that it results from the search for mates by the sexually active individuals, which most often are the pubertal recruits (King, 1983). One prediction of the sexual search hypothesis is that the dispersal rate of all individuals in the population will be positively associated with the level of sexually attractive stimuli present in the environment. These stimuli may be those provided by the sexually active individuals present in the population, but they also include the sexually attractive signals produced by these individuals. Although there is considerable anecdotal reference to the existence of these signals in the environment (e.g. Moore, 1965), little is known about the nature of these stimuli or the modality of their perception. In many rodents, however,

sexual attraction or sexual recognition stimuli are commonly presumed to be odorous substances produced in the preputial gland in both sexes (e.g. Vandenbergh, 1975). If sexually attractive stimuli promote dispersal in sexually active individuals, I predicted that the initiation and rate of juvenile dispersal could be affected by 1) altering the levels of sexually attractive stimuli in the environment and/or 2) manipulating the sexual maturation or sexual behavior of juveniles.

Most P. m. bairdi disperse in the spring and summer when juveniles mature sexually. Dispersal rates in the fall are low, and only adults continue to breed (Howard, 1949; King, 1983). These two seasonal patterns permit an experimental test of the two complementary predictions of the sexual search hypothesis. For spring and summer seasons, I predicted that a reduction in the level of sexually attractive stimuli and/or the prevention of sexual maturation in juveniles would result in lower than normal dispersal rates. Conversely, in the fall, an increase in the level of sexually attractive stimuli and/or number of sexually active juveniles would result in greater than normal dispersal rates.

A field experiment test of the sexual search hypothesis poses several methodological problems. The first concerns the control of other independent variables (e.g. population density, predation pressure, nutrition, and intraspecific competition) which are suspected to be causally related to dispersal. To provide some control of these variables, I introduced structured populations of P. m. bairdi into a study site that was provided with favorable microhabitats consisting of mouse-accessible enclosures with nest-boxes and surplus food and water. A second technical problem involves measurement of dispersal in the

field. I used inter-enclosure movement data and the disappearance of marked individuals from the study area to measure dispersal. Dispersal measured as disappearance, however, was irreconcilably confounded with mortality. Finally, a third methodological problem concerns the selection of techniques for manipulating either the sexually attractive stimuli or the sexual maturation of juveniles. Given that little is known about the nature of sexually attractive stimuli, I chose to manipulate the sexual maturation of juveniles by treatment with exogenous hormones.

Chapter 2 deals with the selection and testing of a hormonal treatment for delaying sexual maturation of juvenile P. m. bairdi. I chose a technique which involved treating mice with melatonin, a hormone with antigonadal properties. It was necessary to learn whether melatonin would be capable of suppressing gonadal development of mice reared under the stimulating influence of a long-day photoperiod. In the laboratory, I performed standard histological examinations of testes and ovaries to assess the antigonadal effects of melatonin treatment on mice reared under the influence of different photoperiods. Specific hypotheses for these treatments are described in this chapter.

Melatonin treatments were used to delay sexual maturation of free-ranging juveniles during the spring and summer. In this experiment (Chapter 3; Experiment 3.1), field-born mice were randomly assigned to either a melatonin or a control treatment group. Stimulation of sexual behavior in free-ranging juveniles was attempted in the fall experiment (Experiment 3.2) by treating mice with exogenous implants of gonadal steriods. The specific hypotheses tested in these experiments are described in Chapter 3.

In the proposed test of the sexual search hypothesis (Chapter 3), I attempted to control intraspecific competition in the population and thus eliminate aggression as a probable cause for juvenile dispersal. Nonetheless, the possibility remained that adult-juvenile aggression (e.g. Fairbairn, 1977a, 1978a) might explain the results predicted for Experiments 3.1 and 3.2. I therefore made direct radiotelemetric observations of the activity patterns of free-ranging adult P. m. bairdi in an attempt to estimate the likelihood of adult-juvenile aggression in the field. The specific hypotheses tested are described in the final chapter (Chapter 4).

CHAPTER ONE
LITERATURE REVIEW
DISPERSAL IN SMALL MAMMALS

Definitions

Any review of small mammal dispersal is beset with problems of terminology. It is difficult to reach a consensus for a definition of dispersal because most interpretations are specifically related to a particular organism or method of study. A commonly used definition is that of Howard (1960, p. 159):

> Dispersal of an individual vertebrate is the movement the animal makes from its point of origin to the place where it reproduces or would have reproduced if it had survived and found a mate.

Howard's definition is certainly consistent with methods of study and results from earlier research on the population biology and social behavior of small rodents, particularly Peromyscus spp. (Burt, 1940; Howard, 1949; Dice and Howard, 1951; Nicholson, 1941). Using nest-boxes in their studies of P. maniculatus bairdi and P. leucopus, these authors found that young mice typically leave the natal nest when they reach sexual maturity, establish a home range of their own away from the place of birth, and remain somewhat sedentary thereafter.

Dispersal has characteristically been reserved to describe the first movements that a young animal makes as it permanently leaves its natal area. Recently, authors have espoused a more dynamic interpretation of dispersal because animals move or change their home range at other times for a variety of reasons (Bekoff, 1977; Gaines and

McClenaghan, 1980; Smith, 1978; Tardif, 1979). Brown (1975:49) viewed dispersal simply as the "movements of animals from a source..." Another widely used and general definition is that of Lidicker (1975:104) who described dispersal as

> ...any movements of individual organisms or other propagules in which they leave their home area, sometimes establishing a new home area...[excluding] short-term exploratory movements.

Even Lidicker's definition may be limiting because it attempts to distinguish between "short-term exploratory movements" from others that are, presumably, dispersal movements. Is it valid to make a distinction between short-term exploratory movements and other, longer movements? I believe not. In some situations, this distinction may have more to do with the methods used to record animal movements and less with the actual behavior of the animals being measured. For example, in live-trap studies, movement distances made by animals can be inferred from straight line measurements made between two trap locations (e.g. Dice and Howard, 1951). These measurements apply to the distance between the two points concerned but not necessarily to the actual distances traveled. Thus, some animals that appear to be making short-term exploratory movements may, in fact, be traveling as far as animals that are classified as dispersers (see Gottfried, 1982).

To define dispersal according to the length and direction of movements is not recommended because these characteristics may also vary from species to species and from individual to individual and, in themselves, do not serve to distinguish dispersal from other movement types (Bekoff, 1977; see also Madison, 1980c). In this review I favor a general definition of dispersal adopted by Gaines and McClenaghan (1980:164, after Endler, 1977) who viewed dispersal as "movements of

only a short distance made by individuals away from a natal site." According to these authors, dispersal movements are "continual rather than periodic and can occur within or between generations." This view of dispersal allows me to consider animal movements without restrictions in their timing or magnitude.

Measurements

Dispersal of individuals or propagules has been demonstrated in some stage of the life cycle of almost every species of plant and animal (Howard, 1960). Although dispersal in small mammals has recently been the focal point of much ecological and behavioral research (Gaines and McClenaghan, 1980), broad generalities of the causes and consequences of this phenomenon have been slow to emerge. This is partly due to inconsistencies in conceptual definitions described above to vague and operational definitions of dispersal. Therefore, before I describe attributes of dispersers and hypotheses proposed to explain the underlying proximal mechanisms of dispersal, I will critically review the methodologies that apply to the study of dispersal.

One fundamental problem with studying dispersal in small mammal populations is a logistic one. Although dispersal is often characterized as involving a series of movements away from a natal site, the processes are difficult to observe directly, particularly among small, secretive, nocturnal mammals. Direct visual observation of these movements is possible in studies of large, diurnal species like ground squirrels (e.g. Armitage, 1973; Carl, 1971; Downhower and Armitage, 1981; King, 1955; Slade and Balph, 1974; Yeaton, 1972). In contrast, small, nocturnal species must be studied by using indirect

methods, such as live-trap sampling of undisturbed or depopulated grids, resource structuring experiments, fenced enclosure experiments, nest-box monitoring, radiotelemetry, radioactive tagging, and other tracking methods (e.g. marked feces, chemically-treated tracking papers).

By using live-trap methods, dispersal can be estimated by sampling individuals that immigrate into a study area. The study area to be monitored can either be left undisturbed as a control, or depopulated (residents removed). In control study areas, newly-recruited (captured) animals can be young animals born in the areas, previously uncaptured older residents, or immigrants. Since it is difficult, if not impossible, to distinguish the source of newly captured animals, dispersal rates can only be estimated. Fairbairn (1977a, 1978a) estimated dispersal rates for P. m. austerus by comparing rates of survival and recruitment of mice within a study area. Fairbairn assumed that high rates of movement by animals within the general population should be reflected in high rates of recruitment and low rates of survival on the control areas. In spite of the difficulties in distinguishing the source of newly-recruited animals, this method has provided insight into the mechanisms of recruitment (Boonstra, 1978; Fairbairn, 1977b, 1978a; Hansen and Batzli, 1978; Sullivan, 1977).

In removal-trapping studies, dispersal rates are estimated in two ways. One assessment of dispersal is made by determining the number of former marked residents of control grids which appear in traps on removal grids. Alternatively, the rate of dispersal can be measured by comparing the number of dispersers which colonize a removal area to the

population density of a control area. Implicit in removal studies are two assumptions: 1) that animals trapped on the removal area are indeed immigrants and not individuals making shorter, exploratory movements from closely surrounding areas (e.g. Stickel, 1946; Joule and Cameron, 1975), and 2) that animals taken from removal grids will not influence the population dynamics of animals from adjacent control grids (Gaines et al., 1979b). Removal-trapping has been the most commonly used method for studying dispersal in small mammals (e.g. Fairbairn, 1978a; Gaines et al., 1979b; Joule and Cameron, 1975; Krebs et al., 1978; Myers and Krebs, 1971; Stickel, 1946; Sullivan, 1977; Tamarin, 1977).

In most removal experiments, the authors assume that removal-trapping measures dispersal patterns that would occur in unmanipulated populations. This method was criticized by Dobson (1981) who argued that removal areas constitute artificial dispersal sinks that may produce a "vacuum effect" (after Gaines et al., 1979a). By comparing dispersal data from removal and non-removal (unmanipulated) study areas, Dobson demonstrated that data collected from removal studies "cannot be assumed to represent an accurate measure of...dispersal...occurring in unmanipulated populations..."

Dispersal has also been studied by restructuring the environment. Gaines et al. (1979b) compared a field burning method with two other experimental techniques (removal-trapping, fenced enclosures) in an analysis of dispersal in fluctuating Microtus ochrogaster populations. The authors found remarkable consistency in the data obtained by the three experimental methods. In this study, the vegetation on two experimental grids was burned, enabling the authors to examine the dispersal of individuals into this suboptimal habitat. A major

assumption of this experiment was that all animals subsequently live-trapped on the burned grids were dispersers. The authors admitted, however, that this assumption was not completely valid because several animals captured on the burned grid were, in fact, residents that survived the burning.

Several investigators have added supplemental food to natural populations of voles and mice and examined the effects of this manipulation on immigration rates and other demographic characteristics (Desy and Thompson, 1983; Flowerdew, 1972; Gilbert and Krebs, 1981; Smith, 1971; Taitt, 1981; Taitt and Krebs, 1981; Taitt et al., 1981). Taitt and Krebs (1981) suggested that experimental structuring of other resources (e.g. estrous females, nest sites) in future studies could lead to a greater understanding of the influences of resource availability on spacing behavior (see also Hypothesis Testing below).

Fenced enclosures have enabled workers to control crucial variables (e.g. immigration rates, predation risk) and identify all individuals that attempt to "disperse" by leaving the enclosure via exit holes or pitfall traps (Gaines et al., 1979b; Riggs, 1979, from Gaines and McClenaghan, 1980). Implicit in this technique is the assumption that all individuals have equal opportunities to "find" the exit holes or pitfall traps. Gaines et al. (1979b) conceded that individuals whose normal home ranges were close to the fence lines and exit holes were more likely than other voles to enter the exit holes.

Fenced enclosures have also provided a method for investigating the role of dispersal as a population regulating mechanism. The enclosure used by Gipps and Jewell (1979) was vole-proof and prevented any immigration or emigration. During the course of their study,

population densities of bank voles (Clethrionomys glareolus) within the enclosure reached extremely high levels, an observation repeatedly observed in other enclosure studies in which dispersal was prevented (Boonstra and Krebs, 1977; Crowcroft and Rowe, 1957; Lidicker, 1976; Krebs et al., 1969).

Drift fences with pitfall traps have been used to study dispersal movements in several species of small mammals, including the old-field mouse P. polionotus (Briese and Smith, 1974; Garten and Smith, 1974). Implicit in all the methods described above which utilize either pitfall traps or exit holes, is the assumption that mice "captured" are actually attempting to exit or enter the study grid.

Recent technological advances in radiotelemetry methods (for reviews see Amlaner and MacDonald, 1979; Cheesman and Mitson, 1982) have permitted detailed investigations of movement and space use by small voles and mice. Radiotelemetry studies have revealed patterns of activity and space-use among free-ranging brown lemmings, Lemmus trimucronatus (Banks et al., 1974), red-backed voles, C. gapperi (Chute et al., 1974; Herman, 1977), collared lemmings, Dicrostonyx groenlandicus (Brooks and Banks, 1971), meadow voles, M. ochrogaster (L.L. Getz, C.S. Carter, pers. comm.), white-footed mice, P. leucopus (Madison, 1977; Mineau and Madison, 1977; B. Ormiston, pers. comm.; Wolff and Hurlbutt, 1982), and deer mice, P. maniculatus (Murphy and Gidner, 1982; Wolff and Hurlbutt, 1982). Compared with live-trapping methods, radiotelemetry techniques provide more precise measurements of an animal's activity and movement. However, radiotelemetric methods have their own limitations. Implicit in these methods is the assumption that they do not interfere with normal behavior and movement

capability. The use of radiocollars could result in reduced activity of monitored animals (Hamley and Falls, 1975; Webster and Brooks, 1980).

In spite of recent improvements in radiotelemetric techniques, few quantitative data are available on the behavior of free-ranging small mammals at the time of dispersal. The lack of information is conspicuous for juveniles, in particular, because of their small size (< 15 g for many mouse-sized species). Most reliable radiotransmitters available on the market today are still too large and heavy to be used for tagging animals that weigh less than 20 g. Given that the predominant dispersers in most small mammals are juveniles, and that radiotelemetric monitoring is not yet feasible for these small-sized animals, it is not surprising that little is known regarding the behavioral attributes of dispersers in the field. Consequently, most radiotelemetry studies are concerned with describing patterns of activity and space-use among free-ranging adults.

In addition to radiotelemetry, remote censusing with radioisotope labels has also contributed to our understanding of movement patterns among free-ranging small mammals. Wolff and Holleman (1978) recommended *in utero* labelings of progeny as a technique for studying kin groups and dispersal of juvenile *Microtus* spp. and house mice, *Mus musculus* from their natal home range. Radioisotope labeling was also used in studies of movement in the field vole, *M. agrestis* (Godfrey, 1954; Myllymäki *et al.*, 1971), Townsend's vole, *M. townsendii* (Hilborn and Krebs, 1976), and coast mole, *Scapanus orarius* (Schaefer, 1982).

A limiting consideration for the use of radioisotope labeling in the study of movements in small mammals is the potential risk that the

associated radiation exposure may produce detrimental effects which could be manifested in behavioral changes (Wolff and Holleman, 1978). Compared with radiotelemetric methods, the monitoring of radioisotope-labeled animals provides only limited information. This is due, in part, to limitations in the distance that Geiger counters can detect radioactively labeled animals. Another drawback is that monitoring is limited to only a few individuals at a time (e.g. Godfrey, 1954).

Patterns of movement and space-use have also been inferred from tracking toe-clipped individuals in a population with the use of chemically treated tracking papers. Space-use by individual M. musculus was determined in a natural population by using a combination of live-trapping and tracking paper methods (Fitzgerald et al., 1981). Spatial relationships among wood mice, Apodemus sylvaticus were inferred from data collected from tracking marked feces (Randolph, 1977).

Finally, the use of nest-boxes in studies of free-ranging Peromyscus spp. has allowed interpretations of animal movements relative to the social and familial history of individuals in a population. Howard (1949), Dice and Howard (1951), and King (1983) used nest-boxes to study dispersal in populations of prairie deer mice (P. m. bairdi). Nicholson (1941) and Trudeau et al. (1980) similarly studied populations of P. leucopus. Most microtines (Microtus spp.) do not regularly use nest-boxes (M. Gaines, pers. comm.), although Gipps and Jewell (1979) reported nest-box use by C. glareolus. The use of nest-boxes is most feasible for Peromyscus spp.

An advantage of nest-box monitoring over live-trapping methods is that nest-boxes do not impose restrictions on movements of mice which

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choose to use them. On the other hand, a mouse which enters a trap and is captured is not only restricted from further movement, but is behaviorally removed from the population until its release. In addition, little is known about how trap spacing or trappability affects behavioral measures (Madison, 1980b). Another advantage of a nest-box study is that it provides an opportunity for determining the birth dates of animals born in the population. With a knowledge of birth dates, the age at dispersal or other events can be determined with reasonable certainty. In live-trapping studies, however, ages can only be estimated (see Attributes of Dispersers below).

The monitoring of animals from birth provides an opportunity for comparing the timing of maturational events (e.g. puberty) with dispersal. For example, an interesting question often asked is whether dispersal precedes the onset of sexual maturation, or vice-versa (see also Attributes of Dispersers below). Thus far, this question has proven difficult to answer in removal studies that utilize live-trapping methods (e.g. Beacham, 1981). If a disperser is trapped in a depopulated grid and found to be in breeding condition, we have no way of determining whether the individual became sexually mature <u>prior</u> to dispersing, or <u>after</u> dispersing but prior to being trapped.

Nest-box monitoring is at a disadvantage when it comes to measuring extensive dispersal movements of individuals which leave the study area (Howard, 1949; King, 1983). Dobson (1981) criticized the use of nest-boxes because he believed that they may influence social pressures that might influence dispersal tendencies. One could also argue that studies which attempt to describe dispersal movements of small mammals with the use of live traps can also be biased. For

example, trappability of deermice has been shown to be a function of the olfactory cues in the traps themselves (e.g. Mazdzer, et al. 1976) and of trap spacing (e.g. Howard, 1949). Despite these criticisms, the use of nest-boxes is recommended in dispersal studies which are planned to allow manipulation or control of resource variables such as nest sites, food, refuges, and protection from predators (see Hypothesis Testing below).

Another fundamental problem with studying dispersal in natural populations lies in our inability to distinguish between mortality or dispersal as the cause of disappearance of animals from a study site. Although Hilborn (1975) experimentally separated disappearance of M. townsendii into dispersal and survivorship components, in most studies investigators do not separate these two sources of disappearance.

Attributes of Dispersers

A fundamental characteristic of all dispersers is their movement. We know about dispersal and associated movements from mapping the pattern of dispersion of individuals in space and time. It is often difficult to determine, from the map alone, either the causes for the observed dispersion patterns, or the perceptual mechanisms which enable the animals to move and to space themselves. Fortunately, we can collect demographic, behavioral, and genetic data which may provide clues to help explain the underlying mechanisms of dispersal. Even with these data, it still seems that much of what we know about the causes of dispersal and spacing patterns in small mammals is like a naive observer's understanding of a game of chess: the players are seen but the rules of movement and the underlying strategies and mechanisms remain obscure.

The study of dispersal is becoming increasingly common and much new data concerning the characteristics of dispersers are being collected. In spite of the variety of life history patterns of the animals studied, some broad generalizations regarding the demographic and behavioral attributes of dispersers are slowly emerging (for other views see Gaines and McClenaghan, 1980; Dobson, 1982).

Sex

In many multiannually cycling species (e.g. *Microtus* spp.) studied, males were the predominant dispersing sex (e.g. Beacham, 1981; Boag and Murie, 1981; Dobson, 1981; Gaines *et al.*, 1979b; Keith and Tamarin, 1981; Krebs *et al.*, 1978; McClean, 1982; Riggs, 1979, in Gaines and McClenaghan, 1980). Tamarin (1977) reported that *M. pennsylvanicus* exhibited shifts in the sex ratios of dispersers, with males predominating in the winter and females predominating in the summer. Seasonal patterns were also described for *M. pennsylvanicus* (Dueser *et al.*, 1981), and cotton rats, *Sigmodon hispidus* (Stout and Demmer, 1982). There were no significant differences reported in sex ratios between dispersers and non-dispersers in *P. maniculatus* (Fairbairn, 1978a; King, 1983) or *P. leucopus* (Nadeau *et al.*, 1981; Tardif, 1979). On the other hand, Gottfried (1982) found male *P. leucopus* to be the predominant dispersing sex.

Age and Weight

Perhaps the most prevalent finding from dispersal studies is the observed movement or disappearance of juveniles from their natal area at, or near, the age of puberty in *P. maniculatus* (Dice and Howard, 1951; Howard, 1949, 1960, King, 1983; Petticrew and Sadlier, 1974), *P.*

leucopus (Hansen and Batzli, 1978; Nadeau et al., 1981), Mus musculus (Anderson, 1970; Myers, 1974), Microtus spp. (Beacham, 1979; Keith and Tamarin, 1981; Webster and Brooks, 1981b), Clethrionomys glareolus (Mazurkiewicz and Rajska, 1975; Wiger, 1982), Sigmodon hispidus (Cameron, 1977), Reithrodontomys fulvescens (Cameron, 1977), Spermophilus spp. (Boag and Murie, 1981; Dunford, 1977; McClean, 1982; Michener and Michener, 1977; Rongstadt, 1965; Slade and Balph, 1974; Yeaton, 1972) and Marmota spp. (Armitage, 1981; Bronson, 1964; Davis et al., 1964).

Although dispersal movements are commonly seen in juveniles, they can also be observed in older animals in P. leucopus (Gottfried, 1982; Stickel, 1946), P. polionotus (Briese and Smith, 1974; Gentry, 1966), Mus musculus (Delong, 1967; Rowe et al., 1964; Strecker, 1954), Microtus spp (Myers and Krebs, 1971; Pucek and Olszewski, 1971; Tamarin, 1977; Van Vleck, 1968), Dipodomys sp. (Fitch, 1948), and Marmota flaviventris (Armitage, 1962, 1977). In some studies, adult dispersers predominated in certain seasons. This has been observed in P. leucopus (Gottfried, 1979), Microtus spp. (Lidicker, 1976), Mus musculus (Newsome, 1969), Tamiasciurus hudsonicus (Kemp and Keith, 1970; Rusch and Reeder, 1978) and Gerbillus allenby; (Abramsky and Sellah, 1982).

In comparing dispersers with residents, dispersers were found to be younger and lighter in weight in P. maniculatus (Fairbairn, 1978a), Microtus sp. (Beacham, 1979; Gaines et al., 1979a; Krebs et al., 1978; Myers and Krebs, 1971; Riggs, 1979, in Gaines and McClenaghan, 1980), Clethrionomys glareolus (Kozakiewicz, 1976), and Sigmodon spp. (Joule and Cameron, 1975; Stout and Demmer, 1982). In other studies of

Microtus, however, the ages of dispersers and residents did not differ (Tamarin, 1977; Verner, 1979, in Gaines and McClenaghan, 1980). In most of these studies, age could only be assessed from measures of body weights or inspection of developmental molts.

Age is probably the most difficult character to measure accurately, particularly in animals from live-trapping studies. Dispersers caught in snap traps and killed can be examined more closely than live animals. Postmortem examinations can provide relatively accurate measurements of age, which can be determined by examining eye lens weights, closure of epiphyseal plates, and dental annulations (Pucek and Lowe, 1975). On the other hand, age determination of live-trapped animals must be based on morphological changes associated with age. Typically, body weight and pelage characteristics are used to define broad age categories (e.g. adult, subadult, juvenile, nestling). Known ages can be assigned to individuals sampled from nest-boxes if the date of birth was previously recorded.

Reproductive Status

According to Gaines and McClenaghan (1980), the reproductive condition of dispersers (regardless of age) showed considerable variation among the species studied. In many species, the reproductive status of dispersing males was a random subset of the resident male population. However, dispersing subadult male M. townsendii (Beacham, 1979, 1981; Krebs et al., 1978), M. ochrogaster (Myers and Krebs, 1971), M. pennsylvanicus (Dueser et al., 1981; Keith and Tamarin, 1981), and M. breweri (Keith and Tamarin, 1981) were more likely to be reproductively active than subadult male residents. Dispersing males of all ages were more likely than residents to be in breeding condition

in C. glareolus (Kozakiewicz, 1976), M. californicus (Riggs, 1979, from Gaines and McClenaghan, 1980), M. breweri and M. pennsylvanicus (Tamarin, 1977).

In reviewing the literature, Gaines and McClenaghan (1980) found no discernible pattern in the reproductive condition of dispersing females. In certain species (M. pennsylvanicus and M. breweri), dispersing females were more likely than resident females to be breeding when trapped (Tamarin, 1977). Nevertheless, in some studies, there was a greater proportion of resident females in breeding condition compared to dispersing females (Myers and Krebs, 1971; Gaines et al., 1979a,b; Keith and Tamarin, 1981). In certain seasons, female P. leucopus dispersers were more likely to be reproductively active than residents (Tardif, 1979). Dispersing female M. townsendii (Krebs et al., 1976), and P. maniculatus (Sullivan, 1977) reached puberty at an earlier age than residents.

Measurement of reproductive condition may also be problematical. For males, the reproductive status can be inferred by measuring the position of the testes. Scrotal testes imply reproductive competence, whereas abdominal testes are indicative of sexually immature status. A critical review of this procedure was provided by Jameson (1950). A more quantitative technique involves laparotomy and the use of a testicular index (Johnston and Zucker, 1980c). This method allows for repeated quantitative assessment of gonadal status but has been reserved mainly for laboratory studies. Repeated and frequent surgical gonadal assessment of males in the field is not recommended.

For females, vaginal patency is used as an indicator of puberty (Clark, 1938; Whitsett and Miller, 1982; for a critical review see

Rogers and Beauchamp, 1974). Pregnancies cannot be verified either visually or by palpation until relatively late in gestation for most small mammals. Parity is difficult to assess for females sampled in live-traps, and is possible for females monitored in nest-boxes only if the female uses the nest-boxes to raise her litters.

Genotype

Electrophoretic analyses of blood plasma proteins revealed genetic differences between residents and dispersers in some species. Myers and Krebs (1971) reported finding differences in the genetic make-up of residents and dispersers at the leucine aminopeptidase (LAP) and transferrin (TF) loci in M. pennsylvanicus and M. ochrogaster populations. Similar results were described for an esterase locus in M. ochrogaster (Pickering et al., 1974), M. pennsylvanicus (Keith and Tamarin, 1981), and M. breweri (Keith and Tamarin, 1981). In contrast to the above studies, Verner (1979, in Gaines and McClenaghan, 1980), and Riggs (1979, in Gaines and McClenaghan, 1980) found no evidence for differential genetic composition in residents or dispersers.

Although much of the work done on genetic analysis of dispersal has been performed on cycling vole species, some analyses have also been done on non-cycling small mammal species. Michener and Michener (1977) found no evidence for a differential loss of genotypes from a population of Richardson's ground squirrels (Spermophilus richardsonii).

Although genetic differences have been found at particular loci, it remains to be shown that these genetic differences between dispersers and non-dispersers are causally related to dispersal, or any other behavior.

Behavior

Field Studies

In natural populations, the behavioral attributes of dispersers can be inferred from direct, visual observations (limited mostly to larger, diurnal species), radiotracking, monitoring of radioisotope-labeled animals, and measurement of skin wounds. Most behavioral measures recorded in the field are related to aggression. The social subordination and genetic behavioral polymorphism hypotheses for a proximal mechanism of dispersal predict that aggressive behavior increases with population density, and interactions between dominant and subordinate animals results in the dispersal of the latter (see Behavioral Hypotheses below). From direct observations of yellow-bellied marmots Marmota flaviventris, Armitage (1973) attributed the dispersal of juvenile males to aggression. A similar pattern was described for male arctic ground squirrels, Spermophilus undulatus by Carl (1971). Pfeiffer (1982) credited aggression as the cause for the disappearance and dispersal of juvenile female Wyoming ground squirrels (S. elegans).

On the other hand, observed aggression in other ground squirrels did not explain juvenile dispersal. In round-tailed ground squirrels, S. tereticaudus, mothers were aggressive only towards non-kin but this did not explain the dispersal of juveniles from their mother's home range (Dunford, 1977). No relationship between aggression and dispersal was detected in populations of Uinta ground squirrels, S. armatus (Slade and Balph, 1974), S. richardsonii (Yeaton, 1972), or M. flaviventris (Svendsen, 1974).

The skins of secretive, small mammals can be inspected, postmortem, for evidence of wounds caused by attacks from other animals (e.g. Rose and Gaines, 1976; Ziesenis et al., 1975). Higher incidences of wounding were recorded as density increased in populations of M. musculus (Rowe et al., 1964; Southwick, 1958), and M. pennsylvanicus (Christian, 1970). Krebs (1964) found higher levels of wounding in lemmings during peak population densities, but when population density declined, levels of wounding remained high. In other microtine species, no relationship between population density and wounding could be found (Batzli and Pitelka, 1971; Rose and Gaines, 1976; see also Laboratory Measures below).

If aggression is indeed an important mechanism for eliciting dispersal in subordinate individuals, and if aggression between dominant and subordinate individuals resulted in wounding and dispersal of the latter, then one should expect to find more incidences of wounding in dispersers than in non-dispersers. I found no evidence from the literature that supports this prediction. Christian (1970, 1971) suggested that subordinate (lightweight?) voles disperse as a result of increased aggression arising from increasing levels of density, but he found no evidence of scarring in dispersers. Furthermore, if lightweight, subordinate individuals are the predominant disperser class (e.g. Baird and Birney, 1982), one would expect to see higher levels of wounding in lighter weight individuals. Rose and Gaines (1976) found no difference, however, in wounding levels of lightweight versus heavyweight M. ochrogaster. The authors suggested that lighter weight voles may not be the predominant dispersers.

Krebs and Myers (1974) discussed the problems associated with collecting and interpreting skin wound data (see also Behavioral Hypotheses: Do They Explain General Attributes of Dispersers? below). In larger, diurnal species like ground squirrels, agonistic interactions can sometimes be visually recorded (e.g. Armitage, 1977; Carl, 1971).

Laboratory Studies

In paired encounters in neutral arena tests in the laboratory, the aggressive behavior of residents and dispersers have been compared. In staging paired encounters, two individuals (usually two males who are strangers) are placed into a "fighting arena" and allowed to interact for a limited period of time. Broad categories of agonistic behavior (Clarke, 1956; Eisenberg, 1963) are recorded for each individual during the test. Myers and Krebs (1971) found no consistent patterns in aggressive behavior for the two Microtus species they studied. Krebs et al. (1978) found dispersing M. townsendii to be more submissive than residents. These authors concluded that dispersing M. townsendii were subordinate individuals, despite finding more wounding in residents than in dispersers. Resident P. m. austerus males were more likely to exhibit aggression during pairwise encounters with a laboratory-trained fighter than dispersing males (Fairbairn, 1978b). Reich et al. (1982) found aggression to be independent of the dispersal rate for male M. breweri.

Laboratory studies have also compared exploratory behaviors of residents and dispersers. Myers and Krebs (1971) found dispersers in M. pennsylvanicus and M. ochrogaster to be less exploratory than residents in a vertical maze test. Fairbairn (1978b) reported similar

results for dispersers in P. m. austerus. On the other hand, in a study of P. leucopus, Tardif (1979) found dispersers to be more likely to cross a water barrier and drop into an unfamiliar area than residents (a measure of exploration). In a test of general activity, dispersing P. m. austerus showed a tendency to be more active than residents (Fairbairn, 1978b), but Myers and Krebs (1971) failed to detect a difference in activity between residents and dispersers in Microtus spp.

Other behaviors have also been examined. Tardif (1979) compared the behavioral responses of residents and dispersers in tests designed to measure the animal's willingness to sample novel fluids and eat a diversity of foods. He hypothesized that mice dispersing across unfamiliar habitat were more likely than residents to encounter unpredictable and novel fluids and foods. Tardif also reported that more field-caught dispersers than residents: 1) sampled novel fluids, and 2) exhibited higher feeding diversity. Savidge (1974) examined social factors which influence the rate at which juvenile P. m. bairdi leave their natal nest site. In his experiments, parents and siblings played important roles in determining the rate of natal dispersal of the juveniles. Juveniles were attracted to their father and typically departed from the natal site with him. Lactating mothers, who were classified as aggressive, increased the rate of departure of their previous litter.

A serious problem with all the studies described above is whether the behavioral tests are valid assays of dispersal-related behavior. The behaviors measured in the laboratory may not be related to the behavior of dispersers in the field (see also Gaines and McClenaghan,

1980). Anderson (1980) criticized the practice of extrapolating conclusions of laboratory arena encounters to natural populations. According to Anderson, the practice of assigning either dominant or subordinate status to animals in the field based on observations of aggression in neutral arenas was "on the par with inferring through observation of boxing matches that there are two kinds of human beings." Furthermore, the relationship between aggression and dominance, and that between aggression and dispersal, has been criticized (Bekoff, 1977; see also review by Bernstein, 1981). There is evidence from studies with rats and other rodents which indicates that aggressive individuals may not necessarily be dominant, and vice-versa (Archer, 1970; Barnett, 1975).

Another problem with laboratory tests is that the conditions of the test are not relevant to conditions that prevail in the field at the time of dispersal. For instance, consider the validity of using only strangers in neutral arena tests (e.g. Krebs, 1970). If individuals who disperse do so as a result of encounters with only strangers, then a test for strangers in a neutral arena is valid. But, suppose would-be dispersers are influenced differently by encounters with <u>familiar</u> individuals than they are by strangers? If would-be dispersers in the field are as likely to interact with familiar animals as with strangers, then how valid are interpretations of data derived from neutral arena tests that only pair strangers? All individuals in the population are not likely to be perceived equally by would-be dispersers. Indeed, Vestal and Hellack (1978) demonstrated that wild-caught <u>Peromyscus</u> spp. are capable of recognizing and distinguishing neighbors from strangers. In this study, strangers were

more likely than neighbors to be aggressive in paired encounter tests (see also Grau, 1982; Halpin, 1981; Kareem and Barnard, 1982; Rajska-Surgiel, 1976). Tests which ignore this behavioral asymmetry are likely to lead to interpretations that have dubious value.

The same can be said for behavioral tests which ignore the experiential history of the tested individuals. Behavioral differences observed between dispersers and residents are likely to be explained by differences in the experiences of these two groups of individuals. For instance, in Tardif's (1979) water barrier test, wild-caught P. leucopus were more likely than laboratory-reared P. leucopus to cross the barriers. In his tests, 42% of the wild-caught mice (n=33) crossed the barriers, compared with only 18% of the laboratory-reared mice (n=62).

In an examination of behavioral development, Tardif and Gray (1978) manipulated the early feeding experiences of two groups of laboratory-reared P. leucopus and later compared their feeding diversity scores with those of wild-caught residents and dispersers. Both laboratory-reared individuals with experience of an unpredictable diet, and wild-caught dispersers, were classified as generalized feeders. Similarly, residents, and laboratory-reared mice exposed to a stable diet were more specialized feeders. From the results of this experiment, we learn that experiences unrelated to actual dispersal may confound the results of tests used to compare the behavior of dispersers and residents.

Despite the limitations described above, several tests did distinguish the behavior of dispersers from that of non-dispersers. Could any of these tests be used to predict, a priori, whether a given

individual is likely to disperse? If a laboratory test were capable of this, it would suggest that some individuals might have a genetic predisposition to disperse as has been suggested by Howard (1960). In a pilot experiment I chose to test the predictability of Tardif's (1979) water barrier test by first testing young field-caught P. m. bairdi in the barrier apparatus and then reintroducing them to their home nest in a field study site (see King, 1983). I tested the hypothesis that mice which cross the barriers in the laboratory would be more likely than non-crossers to disperse after being returned to the field. The results of this experiment were equivocal; barrier-crossing mice were no more likely than non-crossers to disperse (disappear). I observed similar results for a general activity test and Tardif's novel fluid test. The results of these experiments suggest two interpretations. First, animals may have a predisposition to disperse, but the tests chosen were not valid assays of dispersal-related behaviors. Secondly, individuals disperse as a result of unique social and non-social experiences, and not as a result of some predisposition factor.

Behavioral Hypotheses

Three of the five hypotheses for dispersal reviewed below are extensions of behavioral hypotheses proposed to explain the mechanisms underlying population regulation of multiannually cycling species (see Gaines and McClenaghan, 1980). These are the social subordination, genetic-behavioral polymorphism, and presaturation-saturation dispersal hypotheses. Gaines and McClenaghan are commended for their review of the literature and attempt to outline testable and alternative hypotheses that may account for proximal causes of dispersal in small

mammals. Unfortunately, it is difficult to discriminate three of their outlined hypotheses on the basis of predictive value. Compared to the three hypotheses referred to above, the social cohesion and sexual search hypotheses described below offer alternative predictions (see also Table 1).

Social Subordination Hypothesis

In 1970, Christian proposed that intraspecific competition resulting from increases in population density is a "major component of the force to disperse." (p. 85). According to this hypothesis, increasing population density leads to an increase in intraspecific interactions which, in turn, result in increased levels of aggression. The increased levels of aggressive interactions between dominant and subordinate animals may lead to a forced dispersal of the latter. Furthermore, Christian (1971) predicted that levels of aggression would be influenced by the proportion of fertile males in the population. These premises were based on laboratory data showing that agonistic behavior increases with population density (Chitty, 1967; Christian and Davis, 1964). The social subordination hypothesis results in the following predictions (Gaines and McClenaghan, 1980): 1) levels of aggression will be positively associated with population density, 2) dispersal will be more common during phases of peak population density than during phases of increasing or declining density, 3) aggression and dispersal will be influenced by physiological responses to increasing population density, 4) the predominant dispersers will be subadult males that have just reached puberty, and 5) compared with residents, dispersers will be social subordinates.

Table 1.1 Predictions of five behavioral hypotheses for dispersal

	DEMOGRAPHIC PARAMETERS			BEHAVIOR				GENETICS
BEHAVIORAL HYPOTHESES	DENSITY-DEPENDENT	AGE-DEPENDENT	SEXUAL MATURATION	RESIDENT AGGRESSION	SEXUAL ATTRACTION	SPACING BEHAVIORS	WEAK SOCIAL BONDS	INDIVIDUAL GENOTYPE
SOCIAL SUBORDINATION	R	R	F	C		C		
GENETIC-BEHAVIORAL POLYMORPHISM	R	R		C		C		F
PRE-SATURATION - SATURATION DISPERSAL	R	R^{S}		C		C		F^{P}
SOCIAL COHESION		R					F	
SEXUAL SEARCH			F		C			

R = Resulting relationship is predicted
C = Causative relationship is predicted
F = Facilitative relationship is predicted
S = Saturation dispersal only
P = Pre-saturation dispersal only

Genetic-Behavioral Polymorphism Hypothesis

The genetic-behavioral polymorphism hypothesis is a modification by Krebs (1978a, b) of a genetic control hypothesis originally proposed by Chitty (1960, 1967) to explain population fluctuations in microtine rodents. Krebs assumed that spacing behavior (e.g. territoriality, dispersal) regulates population density in microtine rodents. During troughs in the population cycles, population density is low and it is assumed that spacing behavior is at a minimum. During this phase, individuals who are adapted for high reproductive output (increase genotype) are favored. As density continues to increase, levels of intraspecific competition increases, resulting in greater spacing behavior among individuals. At peak densities, intraspecific competition is intense and individuals who are adapted for conditions of mutual interference (high-density genotype) are favored. According to Krebs, it is adaptive for these high-density genotype individuals to be aggressive when resources are limited. He believed that breeding females are the limiting resource and, as density increases, males compete for access to these females. Krebs suggested that during these attempts to acquire breeding females, dominant males interact aggressively with subordinate males, promoting the dispersal of the latter. This hypothesis makes the following predictions (Gaines and McClenaghan, 1980): 1) spacing behavior will occur more frequently at high population density than low density, 2) more dispersal will occur in phases of increasing density than in phases of declining density, 3) spacing behavior, including dispersal, has a large genetic component, and 4) dispersing individuals will be social subordinates.

Presaturation-Saturation Dispersal Hypothesis

This hypothesis predicts that there are two types of dispersal (presaturation and saturation), each corresponding to a different phase in the fluctuating population cycle (Lidicker, 1975). Presaturation dispersal from a population is expected to occur before density reaches the population's carrying capacity. Presaturation dispersal, then, occurs at low density or during the early increase phase. Lidicker (1975;106) suggested that presaturation dispersers are sensitive to changes in population density and, thus, emigrate before "resources... run out for them." On the other hand, saturation dispersers are characterized as "social outcasts, juveniles, and very old individuals, those in poor condition and in general those least able to cope." Thus, saturation dispersal is the emigration of "surplus individuals from a population living at or near its carrying capacity."

This hypothesis makes the following predictions (Gaines and McClenaghan, 1980): 1) dispersers from populations at peak or declining densities are qualitatively different from dispersers from growing populations, 2) presaturation dispersers will be more reproductive and in better condition than saturation dispersers, 3) presaturation dispersers will be more likely than saturation dispersers to survive and reestablish themselves elsewhere, 4) behavior of presaturation dispersers will have a higher heritability than behavior of saturation dispersers, 5) saturation dispersal rates will be positively associated with population density, and 6) saturation dispersers will be socially subordinate to non-dispersers.

Social Cohesion Hypothesis

According to Bekoff (1977), aggressive behavior in many mammals does not necessarily provide an adequate stimulus for dispersal. He

proposed that behavioral interactions occurring prior to dispersal are more important determinants of dispersal patterns than are aggressive interactions occurring "at the time of dispersal." This hypothesis is based on a premise that experiential effects of early agonistic behavior, followed by social play, determines the type of individual that is likely to stay or emigrate. He suggested that individuals who have difficulty developing strong social ties with their siblings or nest mates are the most likely to disperse.

According to Gaines and McClenaghan (1980), the social cohesion hypothesis predicts that: 1) individuals who lack strong social bonds with close relatives are most likely to disperse.

Sexual Search Hypothesis

In a study of dispersal in P. m. bairdi, King (1983) proposed a sexual search hypothesis which predicts that the dispersal rates will increase in direct proportion to the rate of recruitment of sexually maturing individuals into the population. The sexual search hypothesis is similar to Bekoff's social cohesion hypothesis in that they both eschew density as an important factor in controlling rates of dispersal. These two hypotheses similarly predict that all individuals will disperse on their own accord, and not as a result of being driven out by resident adult aggression. Unlike the social cohesion hypothesis, King's hypothesis is unique because it emphasizes the perception by adults, subadults, and sexually maturing juveniles of other sexually active individuals in the population as the stimulus for dispersal in search of mates. In Bekoff's hypothesis, on the other hand, the suggested impetus for dispersal is agonistic behavior occurring during the formation of dominant-subordinate relationships

prior to dispersal. The sexual search hypothesis predicts that: 1) juvenile dispersal rates will be higher during seasons in which juveniles are sexually recruited into the population than during seasons in which juveniles fail to become reproductive, 2) dispersal rate of all individuals in the populations will be positively correlated with the level of sexually attractive stimuli present in the environment, and 3) age of dispersal by young individuals can be experimentally delayed by suppressing their sexual maturation, or advanced by sexual stimulation.

Table 1 summarizes the major predictions of the above hypotheses for the causes of dispersal in small mammals. The first three hypotheses make the same predictions: that dispersal is dependent on density, aggression levels in the population, and age. The social cohesion hypothesis eschews aggression and density as factors which affect dispersal, but predicts that dispersal is an age-dependent phenomenon. The sexual search hypothesis avoids making any systematic predictions regarding the dependency of dispersal on aggression, density, or age.

Behavioral Hypotheses: Do They Explain General Attributes of Dispersers?

How well do these hypotheses explain the general patterns of results obtained from studies on dispersal in small mammals? Here I provide a brief summary of general demographic and behavioral attributes of dispersers, each followed with a critical interpretation of the predictive value of the behavioral hypotheses described above. Finally, I suggest recommendations for more rigorous testing of dispersal hypotheses, specifically, a test of the sexual search hypothesis.

Demographic Generalizations

The social cohesion hypothesis is not considered here because it is primarily concerned with behavioral differences, and was not formulated with attention to demographic measures.

Population Density

As described above, the rate of dispersal for many small mammal species is independent of population density. Even though the number of dispersers is positively correlated with population density, the proportion of dispersers remains relatively constant at all densities. According to Gaines and McClenaghan (1980), the results described above can be partly explained by the genetic-behavioral hypothesis which predicts a greater number of dispersers during phases of increasing density. On the other hand, these authors also believed that these results are inconsistent with the social subordination hypothesis which predicts that dispersal rates should be higher during the peak phase than during the increase phase of a population cycle.

The presaturation-saturation dispersal and genetic-behavioral hypotheses assume that animals are sensitive to changes in population density, and that the tendency for dispersal should increase with increased density. There are several problems with this assumption. An obvious limitation is that dispersal (as measured by the proportion of dispersers in the population) and density are not always correlated. A second concern deals with a misinterpretation of population density. As King (1973) pointed out, density is a convenient term given to an easily measured population variable that is mostly descriptive (e.g. number of individuals in the population per given area). The concept of density does little to explain the relationships of individuals in

the population. As Krebs and Myers (1974) cautioned, we know little of the rules that govern rates of interactions between small mammals in the field. It is difficult to imagine that individuals are basing their decision to disperse on a numerical interpretation of the population instead of on the outcome of social interactions between individuals. As other authors have pointed out, it is the magnitude of social interactions associated with population density, and not density alone, which explains change in behavior such as aggression and activity (Lloyd and Christian, 1967; see also King, 1973; Lloyd, 1980; Tamarin, 1980).

The presaturation-saturation hypothesis also predicts that most dispersers emigrate prior to resource depletion and, thus, are presaturation type dispersers. A limitation of this hypothesis is that it is difficult to distinguish between presaturation and saturation conditions because it is impossible to determine when a population has reached its carrying capacity.

The social cohesion and sexual search hypotheses make no systematic predictions about the relationship between population density and the dispersal rate.

Sex

For multiannually cycling species (many microtines) studied, there was a slight tendency for male-biased dispersal. This pattern was not observed in species, including those of the genus Peromyscus. The pattern with many microtines is best explained by the genetic-behavioral polymorphism and social subordination hypotheses. Even among some of these species, there is a large proportion of female dispersers. The absence of sex-biased dispersal among some Peromyscus

species and certain microtines is consistent with the presaturation-saturation and sexual search hypotheses which predict that dispersers can be of any sex.

Age/Weight

For most species studied, dispersers are predominantly young, lightweight individuals. These results are consistent with the social subordination and sexual search hypotheses. The genetic-behavioral polymorphism hypothesis predicts that dispersers are most likely to be social subordinates. Usually, subordinate individuals are considered to be predominately young and/or lightweight (e.g. Baird and Birney, 1982). Presaturation dispersers are expected to be of any age, but saturation dispersers are likely to be either young or very old.

Reproductive Condition

Despite the species variation in reproductive condition displayed by dispersers, there is a slight tendency for dispersing females to be subadults in breeding condition. This pattern is inconsistent with the social subordination and genetic-behavioral polymorphism hypotheses which predict that dispersers will be less reproductive than residents. In contrast to the social subordination hypothesis, the genetic-behavioral hypothesis predicts that dispersers, though non-reproductive at the time of dispersal, are capable of breeding successfully elsewhere. The results described above for females are best explained by the presaturation-saturation and sexual search hypotheses. Presaturation dispersers are expected to be capable of reproducing, and the sexual search hypothesis predicts that dispersers are individuals who are sexually active. A distinction should be made between

reproductively active and sexually active. The sexual search hypothesis predicts that reproductively active females, especially lactating ones, are essentially forced to be sedentary by their dependent offspring. However, breeding females may be expected to shift nest sites, particularly at the time of weaning their litters (see also Stenseth, 1978).

Behavioral Generalizations

Aggression

Many investigators have claimed that aggression and dispersal are responses to changes in population density. They cite evidence of aggression in laboratory tests and wounding in natural populations in support of their claim. As indicated above, this assertion can be criticized on several grounds. First, the practice of relating changes in behavior to changes in population density is considered by some authors to be invalid (Bekoff, 1977; King, 1973). For instance, density can be a predictor of aggression so long as it can be demonstrated that the frequency of social interactions is at least correlated with density. Second, the methods available for measuring aggression between individuals are fraught with limitations. As indicated above, it is almost impossible to directly observe aggression as it occurs among individuals in the natural population. In fact, even among authors who have implicated aggression as a factor in the regulation of dispersal and spacing behavior in populations, there is an admission that behavioral defense of space has not actually been observed in the field (e.g. Mihok, 1981; Fairbairn, 1978a,b; Baird and Birney, 1982). Much of the evidence for aggression occurring in natural populations is derived from the assessment of skin wounding.

Krebs and Myers (1974) discussed two problems associated with interpreting the significance of skin wounding data. First, a wounding index is only a crude measure of aggression. Others have shown that animals can space themselves without aggression or fighting (e.g. Lorenz, 1973). Second, wounding data confound population density and aggressiveness. According to Gaines and McClenaghan (1980:175), it is difficult to tell if

> the level of wounding is a result of changing density in the population, which in turn promotes interactions among individuals with relatively constant levels of aggressiveness, or whether aggressive behavior actually changes with density.

The data summarized by Gaines and McClenaghan (1980) indicate that population density and estimated levels of aggression for individuals are independent. Furthermore, there is no consistent difference in measured aggression between residents and dispersers. These results are consistent with the social cohesion and sexual search hypotheses which predict that dispersers are individuals who emigrate or move on their own accord, without any presumptive aggressive interference at the time of dispersal. Additionally, presaturation dispersal can also explain these data patterns.

Other Behaviors:

For behaviors that have been observed and measured in at least several different species, there is clearly no relationship with field measures of dispersal. In come species, dispersers had higher scores of general activity and exploratory behavior than residents while in other species the opposite was true. The behavioral hypotheses make no predictions for these behavioral differences. The equivocal nature of

these results is hardly surprising when one considers the inability of laboratory tests to discriminate dispersal-related and non-dispersal-related behaviors (see Behavioral Attributes of Dispersers - Laboratory Measures above).

Some of these hypotheses explain more of the data patterns than other hypotheses. The demographic and behavioral patterns are most consistent with the sexual search hypothesis which predicts that dispersing individuals are likely to be sexually active individuals of either sex. This hypothesis also omits aggression as the critical element in the dispersal process. Despite the apparent general applicability of the sexual search hypothesis, it does not explain all modes of dispersal, which leads us to ask the following question: Can a single hypothesis adequately explain the underlying mechanisms for dispersal in all or most small mammal species? Probably not. In the past, there have been recommendations for universal explanations for dispersal (Howard, 1960) and other, similarly complex phenomena including population cycling in microtines (Kreb and Myers, 1974). In recent years, an increased focus on dispersal research and advances in field-oriented experimental methods, among other things, have led some researchers to espouse "multifactorial" explanations for the proximal causes of dispersal (e.g. Gaines and McClenaghan, 1980; Bekoff, 1977). This recognition is due, in part, to an awareness that there is tremendous between- and within-species variation in life history strategies. For any given individual, the strategy of dispersal is guided by the individual's perception of its ecological and behavioral milieu which may change in space and time. Given the complexity of individuals and their potential for varied responses to environmental

and behavioral stimuli, it is not surprising that many proximal causes may exist for dispersal.

Additionally, the absence of a unifying model may also be due, in part, to our interpretations of the hypotheses themselves (Gaines and McClenaghan, 1980). For example, some of the hypotheses test the same predictions, but do so for different reasons. For instance, the sexual search and social subordination hypotheses both predict that dispersers will be predominantly individuals that are sexually mature (Table 1). The social subordination hypothesis predicts that young, sexually mature individuals disperse as a result of aggressive encounters with adults, whereas the sexual search hypothesis makes the prediction that sexually active individuals disperse on their own accord in search of other sexually active individuals. It is difficult to test and eliminate competing hypotheses which test the same predictions (Gaines and McClenaghan, 1980). This difficulty stems from a more serious problem that is basic to all studies of dispersal: How is dispersal operationally defined? Dispersal means different things to different researchers. To some, it means the disappearance of individuals from a study site; to others, it means the immigration of individuals into a depopulated area. Even if one could agree on an operational definition of dispersal, we are still left with interpreting how and why it occurred. The causes for dispersal, unfortunately, are hidden in other, indirect measures that are difficult to interpret, and multiple interpretations are often possible. For instance, in the example above, two interpretations are put forward to explain the significance of one common observation: dispersing individuals are sexually mature. To some researchers, sexual maturity in young individuals is the

catalyst which provokes aggression by adults, leading to the dispersal of juveniles. To others, sexual maturity is a self-motivating stimulus in a search for mates.

Hypothesis Testing

That unifying principles are lacking may also be due to an absence of rigor in experimental design and testing. A serious criticism of most small mammal population research (of which dispersal is often a part) is that many studies are descriptive, unreplicated, or both (for a critical review see Hayne, 1978). For both descriptive and experimental studies, replication of measurements from individuals, study areas, or populations is necessary to measure variability and improve the precision of observations. Without replication, there can typically be no indication of the precision or generality of the findings (Hayne, 1978). Hayne distinguished descriptive and experimental studies on the basis of whether treatments are arbitrarily imposed upon a given population. Descriptive study allows for observation without interference whereas in experimental study, the researcher introduces a perturbation to observe its effect. Much of our inability to explain dispersal mechanisms stems from the prevalent use of descriptive studies, but where the job is to explain these patterns, the experiment provides the most powerful approach (Hayne, 1978).

Compared with descriptive studies, experimental approaches (sensu Hayne, 1978) to studying dispersal have, until recently, been relatively uncommon. In recent years, experimental methods have been used to investigate the effect on dispersal or social spacing caused by manipulating sex ratios in Microtus populations (Boonstra, 1976;

Redfield et al., 1978); altering the quality or quantity of food in populations of Microtus spp. (Desy and Thompson, 1983; Mares et al., 1982; Taitt et al., 1981; Taitt and Krebs, 1981), Peromyscus spp. (Gilbert and Krebs, 1981; King, 1983; Taitt, 1981), C. gapperi (Gilbert and Krebs, 1981), and Douglas squirrels, Tamiasciurus douglasii (Sullivan and Sullivan, 1982); altering aggression in Microtus species via hormonal modification (Krebs et al., 1977; Taitt and Krebs, 1982) altering perinatal exposure to gonadal steroids in young Belding's ground squirrels (Holekamp, 1982); and tailoring the environment to provide excess refuges in M. townsendii (Taitt et al., 1981), and in semi-natural populations of P. m. bairdi (King, 1983). Boag and Murie (1981) suggested manipulating density of ground squirrel populations and measuring the effect on dispersal rates. Even in experimental studies of dispersal, many potentially crucial independent variables are not properly controlled. In numerous species studied, there are often numerous variables associated with dispersal. These include: season, food supply, competition, aggression, predation, population density, sex, age, and reproductive condition. Many of these variables are correlated with each other which makes adequate control of certain variables more difficult than others.

King (1983) designed a field experiment which allowed partial control of several of these dispersal-related variables in a test of seasonality of dispersal in populations of P. m. bairdi. King argued that this design would allow him to determine, for instance, if seasonal differences in dispersal remained after controlling food availability, then food supply could be eliminated as a factor of proximal control for dispersal in the population studied. By partially

controlling food availability, as well as initial demography, predation, and competition in the study population, King was able to identify social conditions contributing to the seasonal patterns of dispersal, and eliminate other elements that did not do so. In sum, King found that social interactions were important to dispersal. He eliminated aggression, social pressure, territoriality or other spacing behaviors as important factors and proposed that the critical behavior was sexual. The sexual search hypothesis he proposed predicted that rates of dispersal movements increase in direct proportion to the rate of recruitment of sexually maturing individuals. Individuals in the population respond to the seasonal recruitment of sexually maturing individuals by increasing their movements in search of mates.

Although generalizations of behavioral and demographic attributes of dispersers from numerous studies appear consistent with a sexual search model, no one that I am aware of has yet proposed an experimental test of predictions encompassed by this hypothesis.

CHAPTER TWO

EFFECTS OF MELATONIN ON THE REPRODUCTIVE SYSTEM OF P. M. BAIRDI MAINTAINED UNDER DIFFERENT PHOTOPERIODS

Introduction

Evidence from both the laboratory and field indicate that seasonal changes in photoperiod are important environmental cues in the regulation of reproductive development in Peromyscus spp. and other rodent genera (for a review see Zucker et al., 1980). Many have reported that young P. m. bairdi born late in the breeding season during the short-days of autumn, fail to become reproductively active during the season of their birth (Rintamaa, et al. 1976), whereas mice born during the long-days of spring and summer do (e.g. Howard, 1949; King, 1983; Millar et al., 1979; Sadlier, 1969). Laboratory experiments with Peromyscus confirmed that a short-day photoperiod, mimicking the photoperiod of autumn, delays reproductive maturation, whereas long-day photoperiods accelerate reproductive development (Johnston and Zucker, 1980c; Whitsett and Miller, 1982; Whitsett et al., 1983).

To test the sexual search hyothesis of dispersal, I needed a technique for delaying reproductive maturation in juvenile mice during the two seasons characterized by long-day photoperiod: spring and summer. I chose a technique which involved treating the mice with the antigonadal hormone melatonin. The antigonadal properties of melatonin had to be examined for the suppression of gonadal development under the developmentally-stimulating effect of a long-day photoperiod. Thus, the general hypothesis tested in this experiment is that melatonin-

implanted mice maintained under a long-day photoperiod will show a delay in gonadal development compared with control-implanted, long-day mice.

Background

Several techniques have been used in the field to manipulate reproductive behavior or development in small rodents. These methods include castration and treatment with exogenous hormones. Castration has been used in majority of these studies in an attempt to manipulate sexual or aggressive behaviors. This method was used in a study of open-field and aggressive behavior in lab-reared and wild-caught meadow voles, Microtus pennsylvanicus (Turner, et al., 1980). Gipps and Jewell (1979) studied an enclosed population of bank voles, Clethrionomys glareolus, and measured responses of population variables to castrated males.

The number of field studies involving treatment with exogenous hormones is also limited, and most involve treatment with androgens. Reproductive behaviors of male red grouse (Watson, 1970) and sharp-tailed grouse (Trobec and Oring, 1972) were manipulated via treatment with testosterone proprionate. Androgen treatment of small mammals in the field has generally been restricted to studies of aggression in voles (Taitt and Krebs, 1982; Krebs et al., 1977); Gipps, 1982; Gipps et al., 1981). Holekamp (1982) used androgens to study the endocrinology of dispersal in Belding's ground squirrel (S. beldingi). Mestranol, a potent synthetic estrogen and chemosterilant, was used by Howard and Marsh (1969) to inhibit reproduction in rats and voles. Goulet (1979, from Taitt and Krebs, 1982) used this synthetic estrogen to manipulate aggressiveness in female Townsend's voles (M.

townsendii). Other chemosterilants have been used to treat birds (e.g. Potvin et al., 1982; Schaefer et al., 1976).

To test the sexual search hypothesis of juvenile dispersal (King, 1983), I needed techniques that would allow me to experimentally induce: 1) sexual behavior in juveniles born in the autumn, a season in which recruitment of non-reproductive juveniles into the population normally occurs (e.g. Howard, 1949), and 2) a delay in sexual maturation of juveniles born in the spring and summer, seasons in which recruitment of reproductive juveniles into the population occurs (King, 1983; K. Murphy, unpub. obs.).

Induction of Sexual Behavior

In mammals, male sexual behavior is controlled by secretion of testicular hormones (for a review see Larsson, 1979). Clemens and Pomerantz (1981, 1982) administered testosterone to castrated male P. m. bairdi and effectively restored male patterns of sexual behavior. Sexual responses can also be restored to ovariectomized female rodents by exogenous treatment with the ovarian hormone, estrogen (e.g. Clemens and Gladue, 1979; Edwards, 1970). Based on the evidence above, I planned on administering exogenous androgen (testosterone proprionate) and estrogen (estradiol benzoate) to juvenile P. m. bairdi to stimulate sexual behavior of mice in a field test of the sexual search hypothesis (Chapter 3, Experiment 3.2).

Delay of Sexual Maturation

I considered several available techniques for preventing or delaying sexual maturation of mice in the field. Sexual maturation of juveniles could be prevented entirely by pre-pubertal castration or by

treatment with a chemosterilant. Alternatively, gonadal development could be reversed by treatment with a putative antigonadotrophic hormone of the pineal gland, melatonin. Chronic administration of melatonin has been shown to cause gonadal regression in Djungarian hamsters, Phodopus sungorus (Hoffmann, 1973), short-tailed weasels, Mustela erminea, (Rust and Meyer, 1969), southern grasshopper mice, Onychomys torridus (Turek et al., 1976), and white-footed mice, Peromyscus leucopus (Johnston and Zucker, 1980a; Lynch and Epstein, 1976; Margolis and Lynch, 1981).

I used melatonin to delay sexual maturation of juvenile P. m. bairdi for the following reasons. The advantage of castration over hormonal treatments is that it unequivocally prevents any gonadal development and removes the gonadal source of sex steriods. A serious disadvantage of this technique is the requirement of subjecting young mice in the field to surgical trauma. Others have used castration successfully (with little or no mortality due to surgery) with voles (Gipps and Jewell, 1979; Turner et al., 1980), but only males were castrated. The procedure for females involves intraperitoneal surgery. Even if successful surgical procedures were developed for young, pre-pubertal P. m. bairdi, mothers tend to remove sutures from their offspring (R. Hill, pers. comm.) and the nests would be disturbed when the pre-pubertal mice were removed for surgery in the laboratory. I wanted to minimize the disruption of parent-offspring bonds characteristically found in the nest (King, 1983; K. Murphy, unpub. obs.).

Although mestranol has been used successfully to inhibit sexual development (Howard and Marsh, 1969; Goulet, 1979), little is known of the action of this and other antifertility steroids (for a review

see Rudel and Kincl, 1966). Mestranol can be administered via subcutaneous injection, stomach tube, or mixed with food. The best method for application is not clear. Taitt and Krebs (1982) abandoned the injection method after discovering that all of the injected females disappeared from the study grid. They had more success with force-feeding mestranol to the voles.

One of the advantages of melatonin treatment over castration or treatment with mestranol is the ease and safety with which it can be administered to mice. Melatonin is easily administered in the form of subcutaneously placed capsules (Silastic tubing) or implants (e.g., Glass and Lynch, 1982; Johnston and Zucker, 1980a). Glass and Lynch's technique is no more intrusive than a subcutaneous injection. Thus, implanation could easily be done on field animals without having to bring mice into the laboratory.

Aside from the practical considerations of using melatonin to manipulate sexual maturation, I had a strong interest in learning more about the role that melatonin might have in controlling seasonal reproductive cycles. Melatonin has also been implicated as an agent partly responsible for seasonal control of reproductive maturation in Peromyscus spp. and other rodents (see also Discussion below). In P. leucopus and other photoperiodically sensitive species (e.g. golden hamsters, Mesocricetus auratus), exposure to short-day photoperiod elicits gonadal regression and reproductive quiescence (for review, see Reiter, 1974; Zucker et al., 1980). In experiments involving these species, melatonin treatment mimics the antigonadal effects of short-day photoperiod (e.g., Johnston and Zucker, 1980a; Goldman et al., 1979; Tamarkin et al., 1976), suggesting that melatonin transduces

the effects of short-day photoperiod on the reproductive system (see Discussion below). It seemed reasonable, then, to suppress gonadal development experimentally using exogenous treatments of melatonin, an endogenous hormone that may naturally exert control of gonadal development in mice. I decided to use melatonin treatments, contingent upon the verification of antigonadal effects of melatonin in juvenile P. m. bairdi.

When I began this study there were no published reports of an antigonadal effect of melatonin in P. m. bairdi, although J.M. Whitsett and I. Zucker (pers. comm.) have recently and independently concluded that melatonin does, indeed, cause gonadal regression in this subspecies. In most of the studies described above, melatonin caused gonadal regression in mice that were reproductively competent prior to treatment. It remained to be seen whether melatonin treatment could effect a delay in gonadal development of pre-pubertal juvenile P. m. bairdi. I planned an experiment to test the effects of melatonin on the developing reproductive system of juvenile P. m. bairdi.

Materials and Methods

Mice used in this experiment were F-1 laboratory-born offspring of wild-caught Peromyscus maniculatus bairdi. The parental mice were trapped from fields in the vicinity of Michigan State University campus, Ingham County, and had been maintained in the breeding colony room for periods ranging from 6 to 18 months. The parents were housed as bisexual pairs in 13 cm x 28 cm x 40 cm deep plastic cages. Each cage contained wood shavings, nesting material (Nestlets, Ancare Corp.) and ad libitum food (Wayne Breeder Blox) and water. The wood shavings and nesting material were changed biweekly. The room temperature in

the breeding colony was maintained at approximately 23° C and the mice were exposed to 15 hours of white fluorescent light and 9 hours of darkness per day (15L:9D).

Within twenty-four hours after birth, experimental mice and their parents were transferred (in the parent's cage) from the breeding colony to one of two photoperiod treatment rooms. One room had the same 15L:9D photoperiod as the breeding colony room (hereafter referred to as long-day) while the other room had a 9L:15D photoperiod (short-day). Air temperature in both the long- and short-day rooms was maintained at approximately 23°C. Lighting was provided by incandescent bulbs.

Pups were weaned at 21 days of age and were thereafter housed individually in 13 cm x 28 cm x 40 cm deep plastic cages. Each cage contained wood shavings, nesting material, and food (Wayne Breeder Blox) and water were provided ad libitum. Wood shavings and nesting material were not changed during the remainder of the experiment. Twenty-eight mice from the long-day room (12 males; 16 females) and 26 mice from the short-day room (10 males; 16 females) were randomly chosen from among 13 litters (6 short-day; 7 long-day) and randomly assigned to receive either melatonin or blank implants.

Melatonin Implants

The procedure used for preparing implants followed the techniques described by Glass and Lynch (1982). Finely ground melatonin powder (Sigma) was thoroughly and uniformly kneaded into purified white beeswax (Carolina Biological Supply) in a weight ratio of 1 mg melatonin: 4 mg beeswax. This preparation was pressed into a slab 1 mm

thick. An implant tool was fashioned from 26 gauge stainless steel hypodermic needles and 21 gauge stainless steel cannula tubing (Figure 2.1).

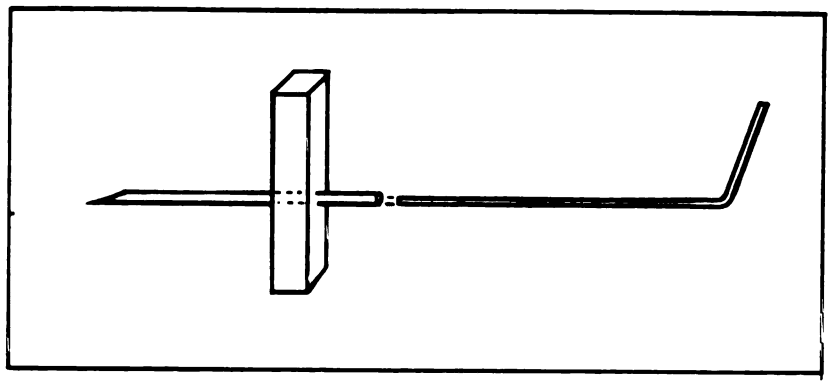


Figure 2.1 Beeswax pellet implant tool.

The plastic sleeve on the blunt end of the hypodermic needle was removed and the needle was given a "handle" by inserting the needle through a small hole in a 25 mm x 15 mm rectangular piece of 1/4" plexiglas and securing it with cyanoacrylate adhesive (Super Glue, Locktite Corp.). The blunt end of the hypodermic tubing was pressed into the prepared beeswax slab and the pellet formed inside the tubing was injected into the animal by means of a plunger fitted into the lumen of the hypodermic tubing. The plunger was fashioned from a length of 21 gauge stainless steel cannula tubing. Pellets prepared with this procedure were 1.0 mm long x 0.8 mm. in diameter. Glass and Lynch (1982), using autoradiographic techniques, found the release rate

of melatonin from 1.0 mm x 0.8 mm pellets to be 10/μg/day from days 1 through 6 post-implantation. The release rates from day 6 through 21 averaged well over 70 ng melatonin/day. These levels were effective in reducing reproductive tract weights in adult female Peromyscus leucopus by 45% relative to controls after 7 weeks of treatment under long-day photo-period (Glass and Lynch, 1982).

Control Implants

Control implants were prepared in the same manner as for melatonin implants with the only exception being that the beeswax contained no melatonin.

Implantation Technique

Each animal was implanted with either a control or melatonin pellet by subcutaneous injection above the interscapular fat pad. Successful implants were confirmed if the pellet could be palpated beneath the skin. All mice were implanted at weaning at a time designated as Day 0. The mice were assigned to the four treatment combinations as follows:

Implant - Photoperiod	Males	Females
MELATONIN-LONG	6	10
CONTROL-LONG	6	6
MELATONIN-SHORT	5	8
CONTROL-SHORT	5	8

A 21-day exposure period was selected for this experiment for the following reasons. Mice from an earlier pilot experiment received a 7-week exposure to one melatonin implant under both long and short-day photoperiods. After 3 weeks of exposure, control females were more

likely than melatonin-implant females to be perforate. However, after 4 weeks of exposure, evidence from examinations of vaginal patency suggested that mice from both control and melatonin-implant groups were no longer different in terms of the number of perforate females. It seemed, therefore, that the likelihood of detecting a delay in gonadal development appeared greatest 2 to 3 weeks after the pellet was implanted in weanlings.

At Day 21, animals were sacrificed with carbon dioxide and the following data collected: 1) body weight to the nearest 0.1 g, and 2) condition of the vaginal orifice (perforate vs imperforate) in females. The animals were then autopsied to determine: 1) the condition of the beeswax pellet, 2) weights of segments of the reproductive tract (ovaries, uterus, and cervix) to the nearest 1 mg, 3) in males, paired testicular weights to the nearest 1 mg. In addition, a testis index (Johnston and Zucker, 1980a) was calculated for each male. The testis index (TI) is deter-mined from the following relationship:

$$TI = \frac{\text{maximum testis length (mm) x maximum testis width (mm)}}{\text{body weight (g)}}$$

The TI has been shown to reflect spermatogenic and steroidogenic function (Rusak and Morin, 1976; Johnston and Zucker, 1980a). Rusak and Morin (1976) report that a TI in excess of 1.8 documents full reproductive potential in golden hamsters, whereas values below 1.0 indicate complete gonadal collapse. For Peromyscus leucopus, Johnston and Zucker (1980a) reported that TI values in excess of 1.7 indicate full reproductive potential, while those less than 1.25 signify an arrest of spermatogenesis.

The testes and ovaries were fixed in Bouin's solution and transferred to 70% ethanol for later histological analysis. Testes and ovaries were dehydrated, embedded in paraffin and sectioned at 7 microns. Sections were stained with hematoxylin and eosin for microscopic examination of spermatogenesis and follicular development.

The functional state of testes was assessed by comparing the testis sections against a spermatogenic and interstitial cell index described by Grocock and Clarke (1974). The spermatogenic index (SI), with values ranging from 0 to 5, gives a measure of seminiferous epithelium activity. A value of 5 represents complete spermatogenesis with large seminiferous tubules and abundant sperm; 4, spermatogenesis is complete, but there are fewer elongated spermatids and spermatozoa; 3, spermatogenesis is incomplete and a further reduction in spermatozoa and spermatids is evident; 2, only round spermatids are present; 1, only Sertoli cells, primary spermatocytes and spermatogonia are present; 0, only Sertoli cells and spermatogonia still occur. The interstitial cell index (ICI), with values ranging from 1 to 5, gives an assessment of the functional state of interstitial tissue, the site of steroidogenesis in the testis (Turner and Bagnara, 1976). This index is based on the assessment of the size of the Leydig cell patches and on the shape of the nucleus within those cells. A value of 5 corresponds to interstitial cell patches that are very large and contain cells with round nuclei, while the value of 1 represents very small patches with cells containing elongate nuclei.

The state of follicular development in ovaries was measured by comparing ovarian sections against a follicular index (FI) proposed by Pedersen and Peters (1968). The follicular classification is based on

oocyte size, follicle size, and follicle morphology. This index has values for follicle that range from Type 1 to Type 8. Type 1 represents a small oocyte with no follicular cells attached, while a Type 8 represents a large, preovulatory follicle. Ovarian sections were scored according to the presence of the most advanced follicle type. In addition, the presence or absence of postovulatory follicles (Graafian) or corpora lutea was noted. All index scores for males and females were based on the inspection of two slides per animal. Each slide contained approximately 18 serial sections from either a testis or ovary. Sections from testes and ovaries of mice were scored without current knowledge of the treatments each mouse had received.

Analysis

The primary dependent variables in this analysis were body weight of both sexes, vaginal patency, reproductive tract weight, and presence of corpora lutea in females, and paired testes weight, and testis index score for males. The specific hypotheses tested here are:
Females treated with melatonin under a 21-day exposure to long-day photoperiod:

1. will have lighter reproductive tract weights relative to control, long-day females.
2. are less likely to become perforate compared with control, long-day females.
3. are less likely than control, long-day females to exhibit corpora lutea in the ovaries.
4. are not expected to have body weights that differ from control, long-day females.

The same predictions above are held for melatonin-implanted, short-day females compared with control-implanted short-day females.

Males:

Males treated with melatonin under a 21-day exposure to long-day photoperiod:

1. will have lower paired testes weights relative to control, long-day males.
2. will have lower TI scores compared with control, long-day males.
3. are not expected to have body weights that differ from control, long-day males.

The same predictions above are held for melatonin-implanted, short-day males compared with control-implanted short-day males.

The data were analyzed with a 2 x 2 analysis of variance for unequal but proportional subclass sizes (Sokal and Rohlf, 1969). A chi-square test for independence was used to establish the effects of the treatments on the number of females with: perforate vagina, corpora lutea.

Results

Two mice (1 control, short-day female, and 1 control, long-day male) died before the experiment was completed.

Males

Testes Weight

The analysis of variance on testicular weights indicated a significant main effect of photoperiod ($F = 5.73$; $df = 1/16$; $p < 0.05$)

with mice from short-day photoperiod having lower testicular weights than long-day mice (Figure 2.2). The main effect of hormone treatment was also significant ($F = 6.98$; $df = 1/16$; $p < 0.05$). Mice implanted with melatonin had lower testicular weights than control-implanted mice (Figure 2.2). There was no significant interaction between photoperiod and hormone treatment (Table 2.1).

Table 2.1 Analysis of variance of testes weights

Analysis of Variance

Source of Variance	DF	MS	F	PROB
Hormone Treatment	1	69.71	6.98	$p < 0.05$
Photoperiod	1	57.29	5.73	$p < 0.05$
Hormone Treatment X Photoperiod	1	3.49	0.35	NS
Error	16	9.99		
Total	19			

Testicular Index

An analysis of variance on TI scores revealed a highly significant main effect of photoperiod ($F = 8.57$; $df = 1/16$; $p < 0.01$), with mice from short-day photoperiod having lower TI scores than long-day mice (Figure 2.3). The main effect of hormone treatment was also significant ($F = 7.84$; $df = 1/16$; $p < 0.05$). Melatonin-treated males had significantly lower TI scores than control-treated males (Figure 2.3). No significant interaction between photoperiod and hormone treatment was observed (Table 2.2).

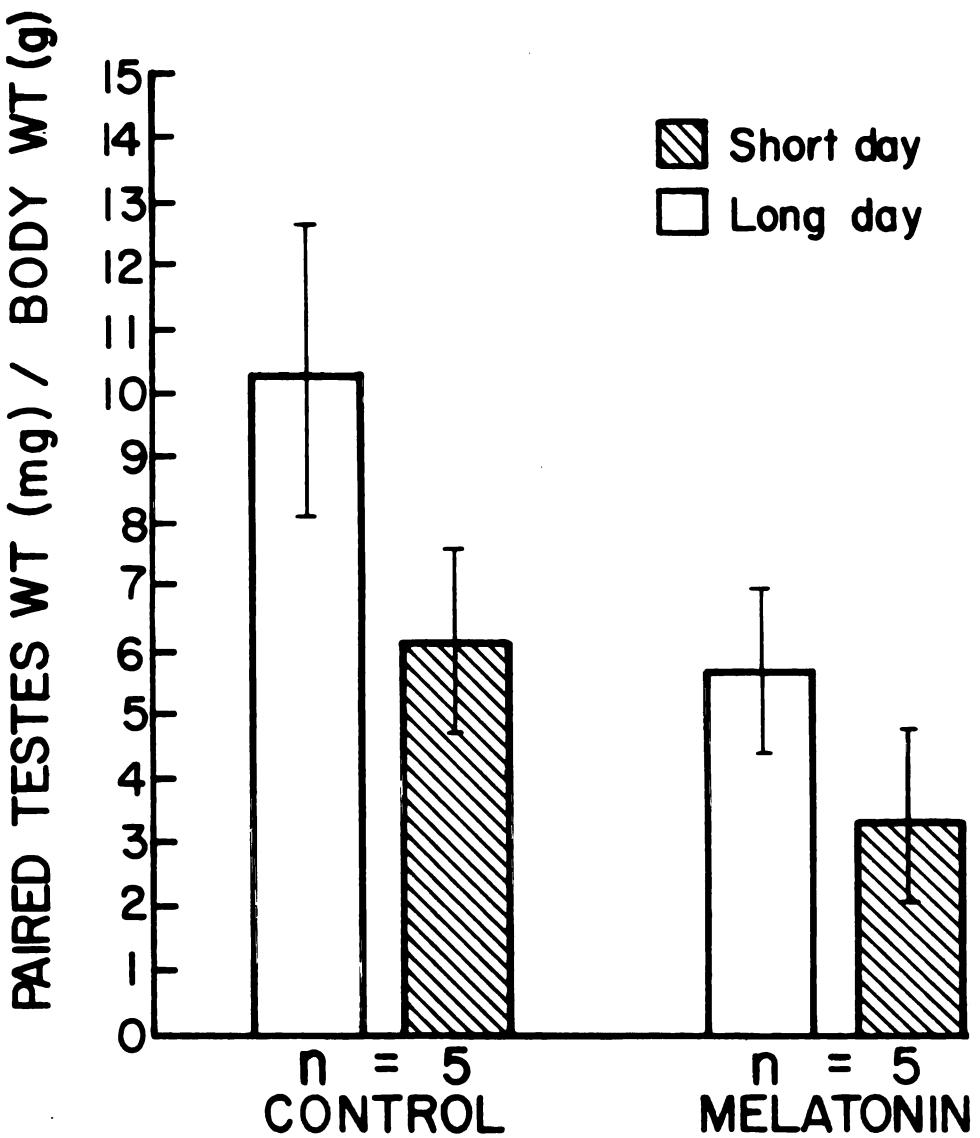


Figure 2.2 Mean paired testes weights. Vertical lines indicate $\pm$ 1 S.E.

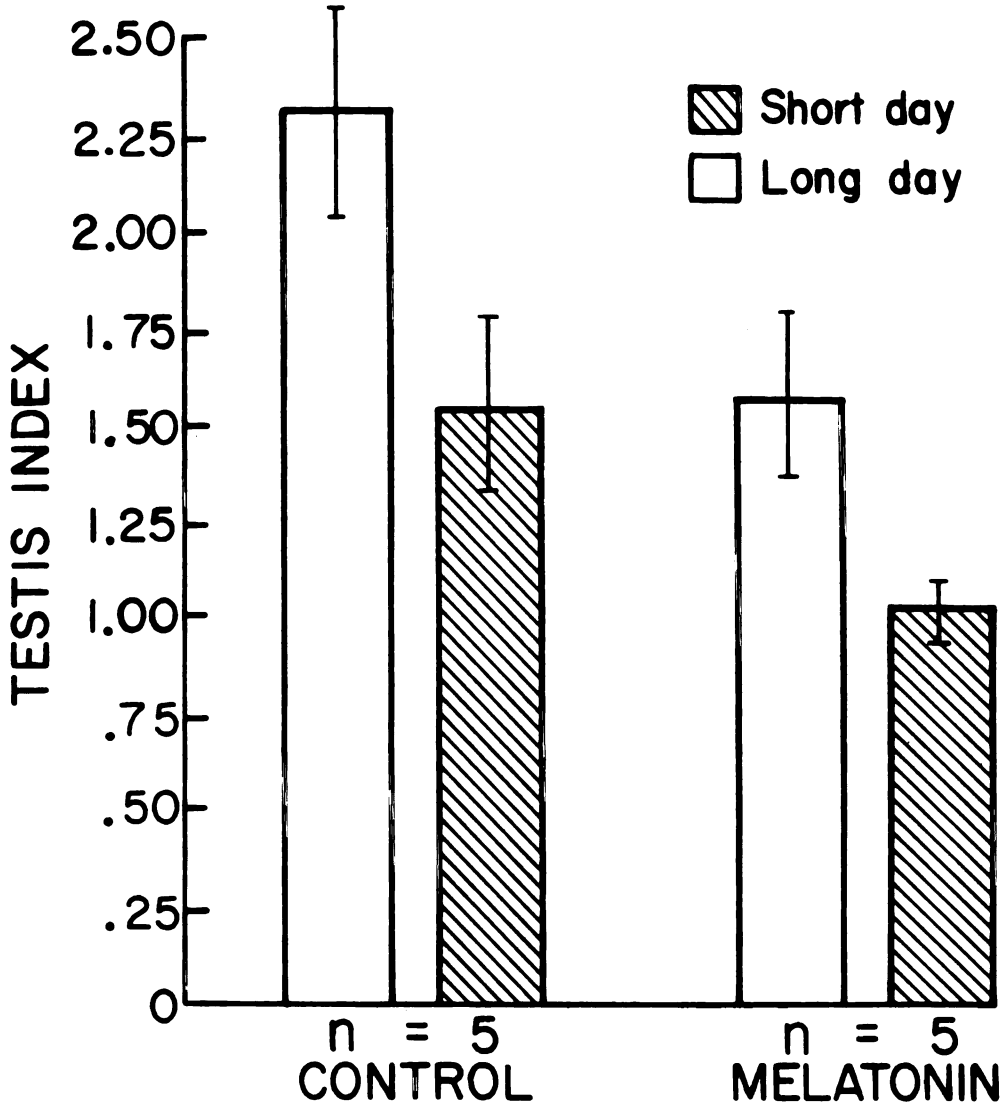


Figure 2.3 Mean testis index scores. Vertical lines indicate $\pm$ 1 S.E.

Table 2.2 Analysis of variance of testes index score

Analysis of Variance				
Source of Variance	DF	MS	F	PROB
Hormone Treatment	1	2.03	7.84	$p < 0.05$
Photoperiod	1	2.22	8.57	$p < 0.01$
Hormone Treatment X Photoperiod	1	0.08	0.31	NS
Error	16	0.26		
Total	19			

Only control-implanted, long-day males had TI values ($\bar{x}$ = 2.33 $\pm$ 0.27 (S.E.)) greater than 1.7, which indicates fully functional gonads in P. leucopus. The melatonin-implanted, short-day mice had TI values ($\bar{x}$ = 1.03 $\pm$ 0.10 (S.E.)) below 1.25, the value signifying spermatogenic arrest.

Histological Assessment of Gonadal Condition

Complete spermatogenesis (stages 4 and 5 as defined by Grocock and Clarke (1974); see Materials and Methods) was observed in 67% of the control-implanted long-day males. In contrast, only 20% of the melatonin, long-day males, and none of the short-day males (control or melatonin-implanted) manifested complete spermatogenesis. Figure 2.4 provides a comparison of the mean SI values for all treatments. Figure 2.5 provides a comparison of mean ICI values for all treatments. An ICI value of 3 or better was observed in 100% of the control, long-day males and 60% of the control, short-day males. In contrast, a score of 3 was recorded in only 20% of the melatonin, long-day males, and in none of the melatonin, short-day males.

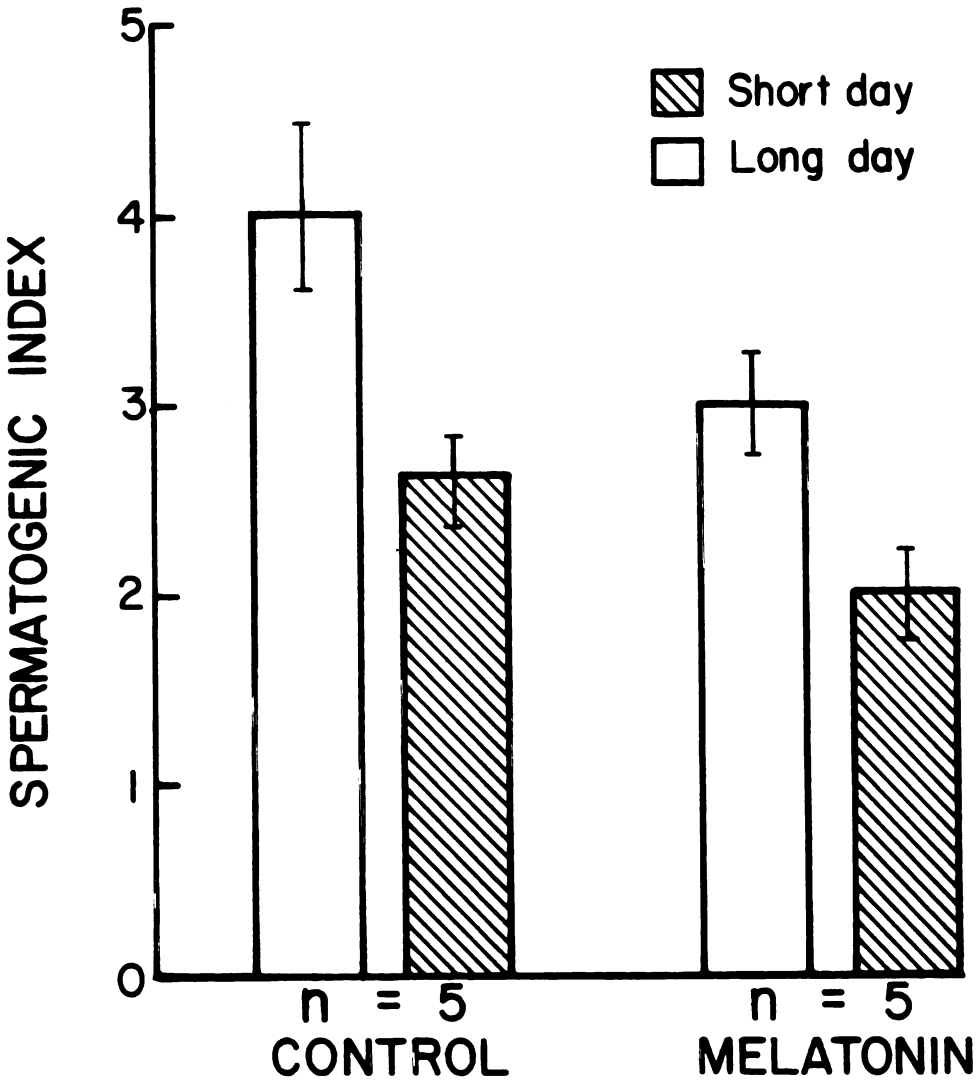


Figure 2.4 Mean spermatogenic index scores. Vertical lines indicate ± 1 S.E.

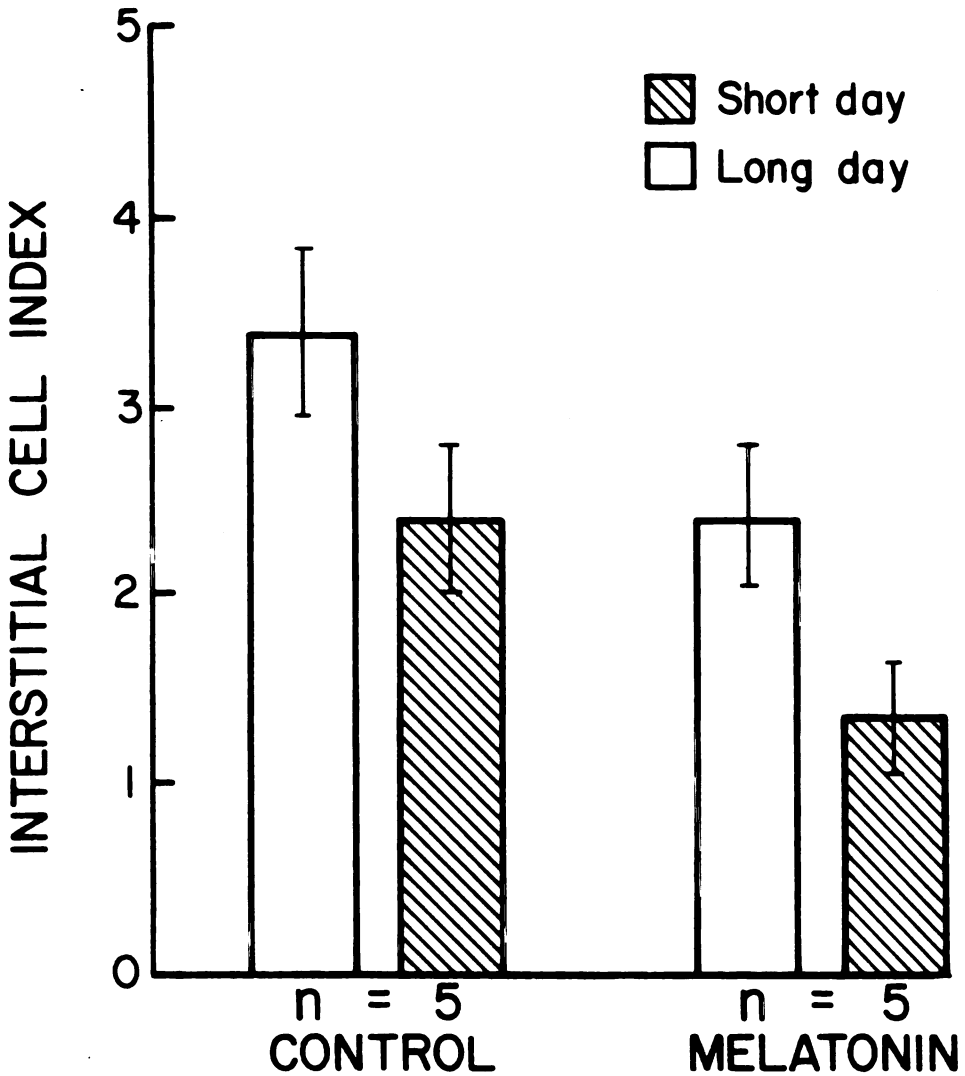


Figure 2.5 Mean interstitial cell index scores for males. Vertical lines indicate $\pm$ 1 S.E.

Body Weight In Males

The analysis of variance on body weights revealed that both main effects of photoperiod and hormone treatment, and their interaction were nonsignificant (Table 2.3; Figure 2.6).

Table 2.3 Analysis of variance of body weights of males

Analysis of Variance

Source of Variance	DF	MS	F	PROB
Hormone Treatment	1	5.52	2.34	NS
Photoperiod	1	0.02	0.01	NS
Hormone Treatment X Photoperiod	1	0.005	0.002	NS
Error	16	2.36		
Total	19			

Females

Vaginal Patency

The null hypothesis that vaginal patency was independent of treatment was rejected ($X^2 = 11.00$; $df = 3$; $p < 0.025$). The control, long-day females had a higher percentage of perforate females than any other treatment group (Table 2.4).

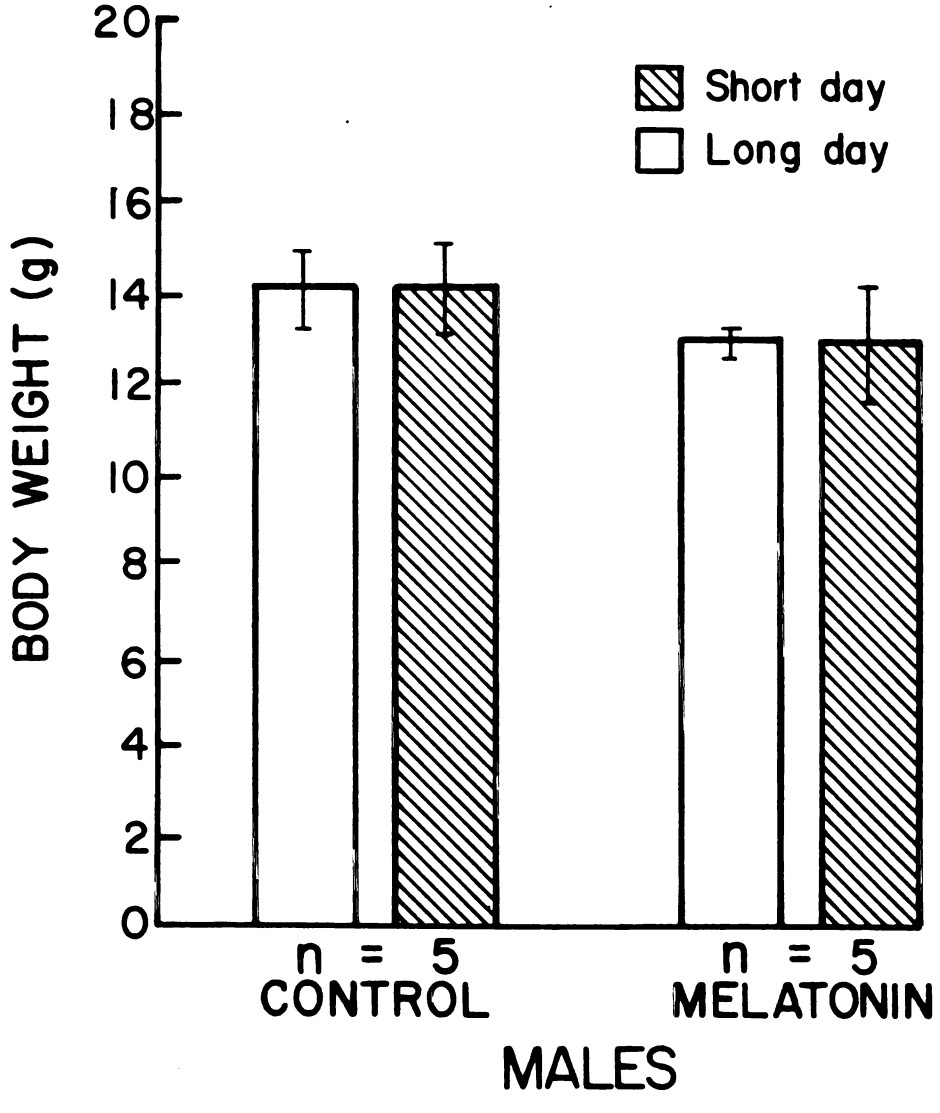


Figure 2.6 Mean body weights of males. Vertical lines indicate ± 1 S.E.

Table 2.4 Frequencies with which females were perforate or imperforate at the end of the 3-week treatment period.

	Treatment Combination			
Response	Melatonin Short-Day	Melatonin Long-Day	Control Short-Day	Control Long-Day
Perforate	0	3	2	5
Imperforate	8	7	5	1
Totals	N=8	N=10	N=7	N=6

$X^2 = 11.00$, df = 3, $p < 0.025$

Reproductive Tract Weight

An analysis of variance on reproductive tract weights indicated a significant main effect of hormone treatment ($F = 5.55$; df = 1/24; $p < 0.05$), with females receiving melatonin implants having lower reproductive tract weights than control females (Figure 2.7). Neither the photo-period main effect nor the interaction of photoperiod x hormone treatment was significant (Table 2.5).

Table 2.5 Analysis of variance of reproductive tract weights of females

	Analysis of Variance			
Source of Variance	DF	MS	F	PROB
Hormone Treatment	1	13.83	5.55	$p < 0.05$
Photoperiod	1	1.70	0.68	NS
Hormone Treatment X Photoperiod	1	0.61	0.24	NS
Error	24	2.49		
Total	27			

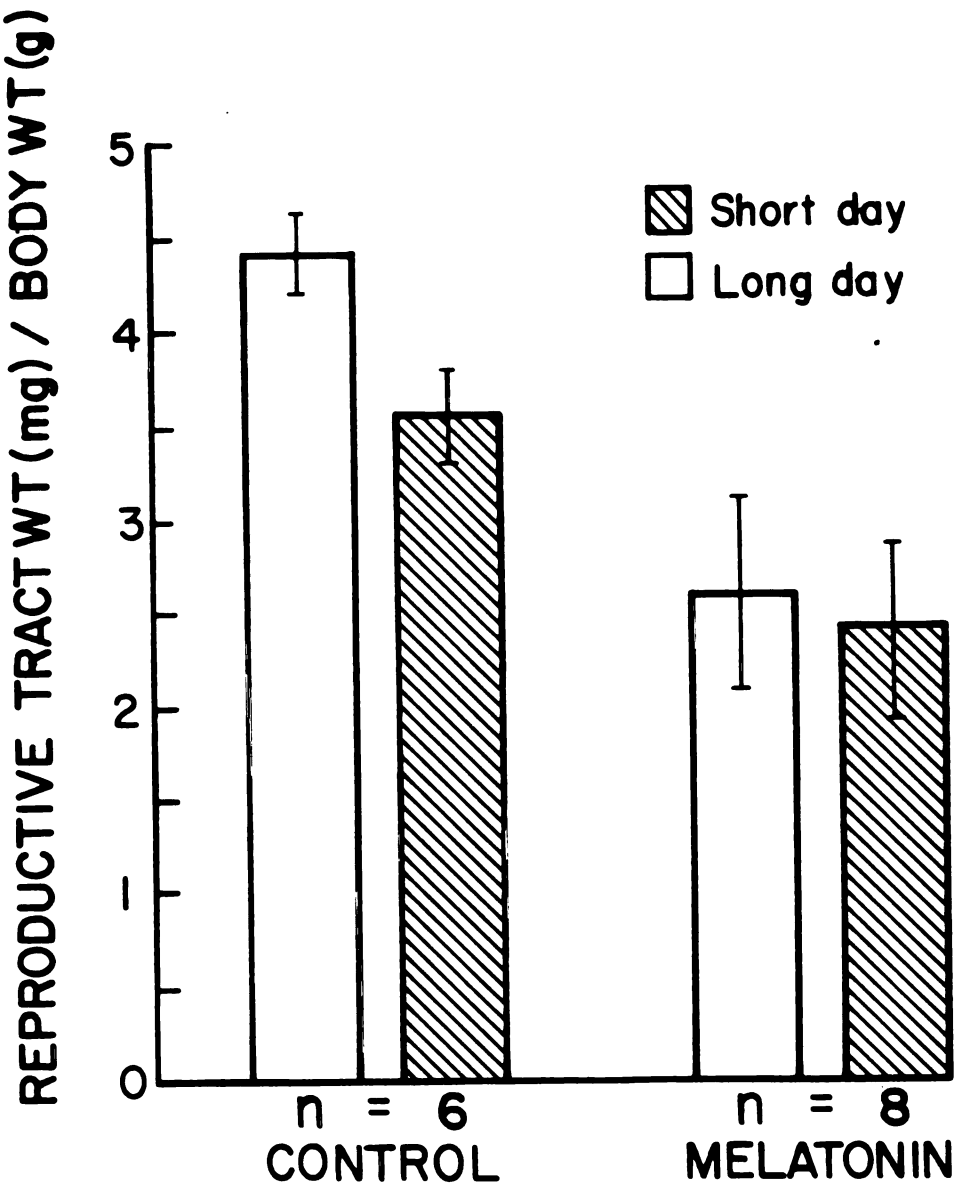


Figure 2.7 Mean reproductive tract weights of females. Vertical lines indicate $\pm$ 1 S.E.

Histological Assessment of Follicular Development

Histological examination of the ovaries revealed that, for females in all treatment groups, follicular development was advanced beyond Type 6 of the Pedersen and Peter's index (Figure 2.8). The Pedersen and Peter's index is based primarily on an assessment of the most advanced follicle observed. Although all mice from the 4 treatment groups had equally advanced follicles, total follicle number differed. Many of the melatonin-implanted females had smaller ovaries and, therefore, fewer, albeit advanced, follicles. Rather than utilize absolute number of follicles as a measure of follicular development, I chose, instead, to score ovaries *a posteriori* according to whether *corpora lutea* were present or absent. The presence of *corpora lutea* indicate that ovulation has indeed occurred. The null hypothesis that presence of *corpora lutea* is independent of treatment was rejected ($X^2 = 8.50$; $df = 3$; $p < 0.05$). *Corpora lutea* were observed in more than 50% of the females from control, long-day and control, short-day treatments. In contrast, *corpora lutea* were present in only 3 of 18 melatonin-treated females (Table 2.6).

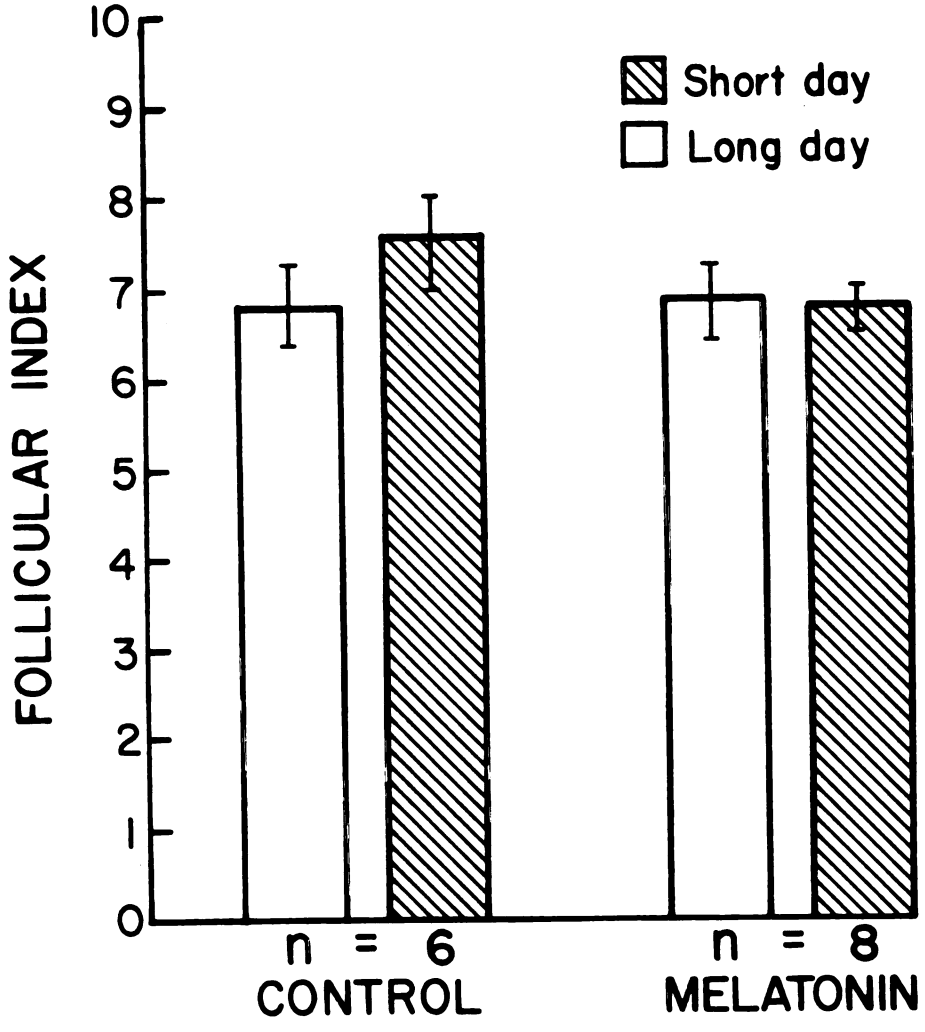


Figure 2.8 Mean follicular index scores. Vertical lines indicate ± 1. S.E.

Table 2.6 Frequencies with which females possessed corpora lutea at the end of a 2-week treatment period.

	Treatment Combination			
Response	Melatonin Short-Day	Melatonin Long-Day	Control Short-Day	Control Long-Day
Corpora Lutea Present	0	3	4	4
Corpora Lutea Present	8	7	3	2
Totals	N=8	N=10	N=7	N=6

$X^2 = 8.50$, df = 3, $p < 0.05$

Body Weight In Females

The analysis of variance on body weight revealed that both main effects and their interaction were nonsignificant (Table 2.7; Figure 2.9).

Table 2.7 Analysis of variance of body weights of females.

	Analysis of Variance			
Source of Variance	DF	MS	F	PROB
Hormone Treatment	1	0.39	0.12	NS
Photoperiod	1	6.51	2.00	NS
Hormone Treatment X Photoperiod	1	0.71	0.22	NS
Error	24	3.25		
Total	27			

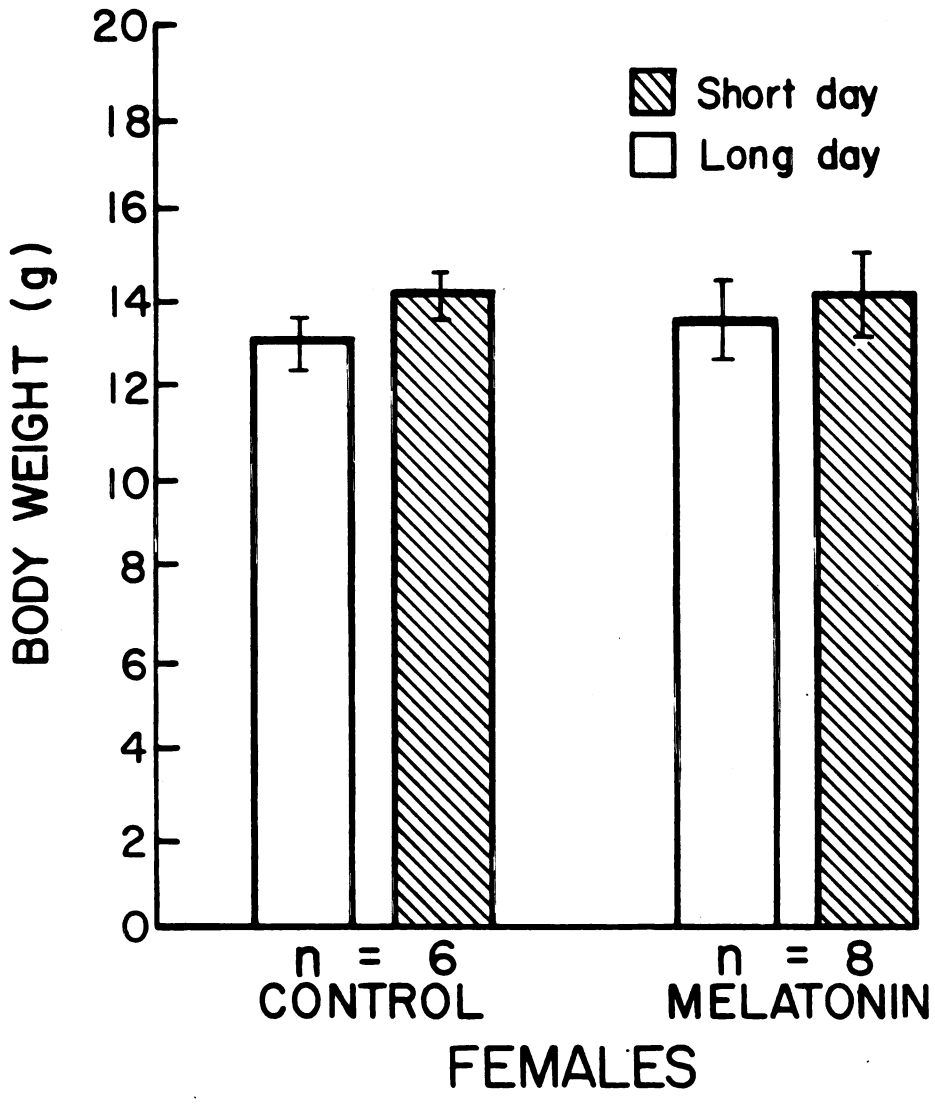


Figure 2.9 Mean body weights of females. Vertical lines indicate $\pm$ 1 S.E.

Discussion

Three weeks of melatonin treatment suppressed gonadal development in juvenile male and female P. m. bairdi raised from birth under either long-day or short-day photoperiods. In males, melatonin suppressed testis growth and inhibited spermatogenesis. The effect observed in this experiment was similar to the results obtained by treating post-pubertal P. leucopus males with melatonin and measuring the extent of gonadal regression (Johnston and Zucker, 1980a; Margolis and Lynch, 1981). From the ICI scores, it appears that interstitial cell activity in males treated with melatonin is reduced compared to control-implanted males (Figure 2.5). Although it is clear that Leydig cells are an important source of steroid hormones, it is difficult to assess accurately steroidogenic activity based simply on histological examination of these cells. Leydig cells are difficult to distinguish from connective tissue elements, and therefore, estimates of steroidogenesis founded on interstitial cell patch size remain very subjective (Turner and Bagnara, 1978). There is evidence, however, from studies with male rats indicating that melatonin inhibits testosterone and androstene-dione synthesis in the testis (Ellis, 1969). Melatonin is believed to exert its antigonadal effects by altering patterns of gonadotrophin secretion (particularly LH) from the hypothalamus (e.g. Cardinali and Vacas, 1978; Kao and Weisz, 1977; Reiter, et al., 1976).

In females, melatonin suppressed growth of the reproductive tract. The melatonin-treated group also had a higher percentage of imperforate females than did the control-treated group. These two results are similar to results from a previous study with P. leucopus (Margolis and

Lynch, 1981). The use of vaginal patency as a valid measure of reproductive condition in mice has been questioned by some (e.g. Rogers and Beauchamp, 1974). Nevertheless, Lombardi and Whitsett (1980) and Whitsett and Miller (1982) found, for female P. m. bairdi, that vaginal patency is a valid measure of gonadal maturation. They based their conclusions on a comparison of reproductive organ weights and vaginal condition.

Both melatonin and control-implanted groups had well developed follicles. This result was not expected and differed from the findings of Lynch and Margolis (1981) for P. leucopus. In that study, none of the females that received a maximum melatonin dose had follicles advanced beyond Type 5b of the Pedersen and Peter's index. For some unknown reason, follicular development proceeded equally for both melatonin and control-treated females in the present experiment. Nevertheless, the ovaries of control-treated females were more likely than melatonin-treated to possess corpora lutea. The presence of corpora lutea is a valid indicator of estrous cycling in this subspecies (e.g. Clark, 1938). Judging by the absence of corpora lutea, a majority of the melatonin-treated females had not begun cycling by 42 days of age.

Under both long and short-day photoperiods, control-treated males and females attain puberty earlier than melatonin-treated mice. These observations provide evidence that the action of melatonin on gonadal development in P. m. bairdi is independent of photoperiod. However, it is possible that the extent of the developmental suppression does depend on photoperiod since short-day photoperiod males treated with

melatonin had lower testicular weights and TI scores than long-day mice treated with melatonin (Figures 2, 3).

A question not answered by this experiment concerned the age at which melatonin-treated mice would attain reproductive competence equivalent to that of their control-implanted counterparts. I conducted an earlier pilot experiment using the same methods used in the present study except that mice received one implant for a seven week period instead of three weeks. After seven weeks, comparisons of gonadal weights, TI and FI scores for melatonin and control-treated mice revealed no significant differences. Thus, it appears that melatonin treatment of 21 day-old mice delays gonadal development for approximately 3 weeks, rather than permanently arresting it.

Body weights of melatonin- and control-treated mice did not differ (Figure 2.6). Lynch et al. (1978) reported a slight decrease in food consumption and lower body weight for melatonin-treated P. leucopus compared to controls, though these differences were not statistically significant.

Regardless of hormone treatment, males maintained under a short-day photoperiod since birth exhibited less gonadal development compared with males from a long-day photoperiod treatment. This reduced development was evident in lower testicular weights and lower testicular index scores. Similar results were reported for male P. leucopus (Dark et al., 1983; Whitsett and Lawton, 1982; Whitsett et al., 1983). Gonadal development in the melatonin-treated long-day males and control-treated short-day males was equally suppressed (Figures 2.2-2.5). This suggests that melatonin treatment mimics the effect of short-day photoperiods on gonadal development in males. This

effect was also observed in P. leucopus (Johnston and Zucker, 1980a) and hamsters, Mesocricetus auratus (Goldman et al., 1979).

Gonadal development in females, on the other hand, was not affected by photoperiod. This result was not predicted. In the present experiment, gonadal development was not suppressed in females reared under a 10L:14D photoperiod, whereas sexual maturation was delayed in females raised from birth under a 8L:16D photoperiod (Whitsett and Miller, 1982). This difference could be due to the differences in the light:dark phases in the photoperiods used in the two experiments. Perhaps a 10L:14D photoperiod is not capable of suppressing gonadal development in females.

Whitsett and Miller (1982) reported an inhibition of sexual maturation in female P. m. bairdi raised from conception or birth under a short-day photoperiod (8L:16D), but no delay in females exposed to the same short-day photoperiod beginning at weaning. These authors suggested that there may be age differences in photoperiod sensitivity, though further research is needed to elucidate this phenomenon.

Body weights of short-day and long-day mice did not differ (Figure 2.6). A similar result was reported for P. m. bairdi females (Whitsett and Miller, 1982) and males (Whitsett et al., 1983).

A significant observation in this and other studies is that a small porportion of mice (5-30%) fail to undergo gonadal regression, even with exposure to a short-day photoperiod or melatonin (Desjardins, 1981; Desjardins and Lopez, 1983; Johnston and Zucker, 1980b; Lynch, 1973). These unorthodox responses by certain individuals may reflect a differential sensitivity to the external cues that evoke gonadal involution (Desjardins and Lopez, 1983; see also Whitsett and Lawton,

1982). For example, in studies which have examined gonadal responsiveness to different photoperiods, it has been typical for other external cues, that could potentially evoke reproductive responses, to be ignored (e.g. Lynch, 1973). Desjardins and Lopez (1983) examined pituitary- testicular functions in male P. m. bairdi exposed to 3 environmental cues (photoperiod temperature, food availability) and found that an individual's testicular response to a short-day photoperiod is dependent on its sensitivity to not only photoperiod, but temperature and food deprivation as well. For instance, they reported that spermatogenesis is influenced by cold temperatures only if males are simultaneously exposed to a short-day photoperiod. An understanding of this differential cue sensitivity phenomenon will be helpful in interpreting variation in responses to treatment in the field experi-ments described in the next chapter (Chapter 3).

Results of this experiment indicate that melatonin effectively delays gonadal maturation in male and female P. m. bairdi maintained under a long-day photoperiod. Therefore, melatonin implants should effectively delay gonadal maturation in mice born in the field during the long-days of spring and summer. The use of this procedure to delay gonadal maturation of mice in a test of the sexual search hypothesis is described in Experiment 3.1 (Chapter 3).

CHAPTER THREE

EXPERIMENTAL TEST OF THE SEXUAL SEARCH HYPOTHESIS OF DISPERSAL IN A SEMI-NATURAL POPULATION OF P.M. BAIRDI

Introduction

This chapter describes two complementary experimental tests of the sexual search hypothesis. In the first experiment (3.1) I tested the prediction that a delay in sexual maturation among field-born juveniles in the spring and summer would result in a delay in or a prevention of their dispersal from their natal site. Conversely, in the second experiment (3.2) I examined whether an increase in sexual activity among juveniles born in the fall would stimulate their dispersal. With the exception of an introductory section describing the general materials and methods for these two experiments and a common discussion section, the results of the two experiments are described separately.

General Materials and Methods

The study grid was located on Michigan State University's south campus in a 40 hectare old-field bordered on the south, east, and north by three roads, Sandhill, Hagadorn (Figure 3.1), and Interstate 96, respectively. A large, mixed-hardwood woodlot served as the western boundary. The nest-box study grid (described below) occupied 1.4 hectares on the eastern edge of the old-field. Dense stands of canarygrass (Phalaris spp.) and quackgrass (Agropyron spp.)

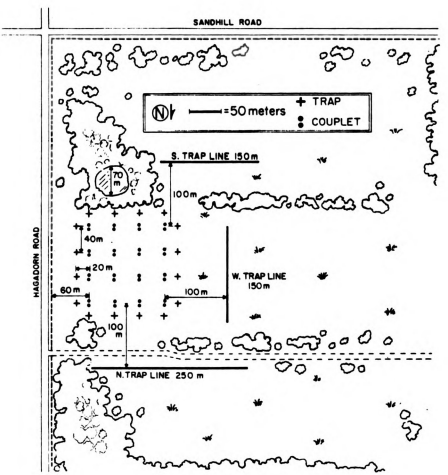


Figure 3.1 Map of the mouse cities study area.

predominated, with interspersed patches of Solidago spp., Daucus carota, Cirsium vulagare, Aster spp., and Rubus spp. occurring secondarily. Small stands of Acer negundo and Populus deltoides were located to the north of the study grid and several small trees of these species were interspersed throughout the grid. Two fence rows of mature trees and shrubs were located to the south and north of the study grid. An ephemeral pond, varying seasonally and annually in size and water depth, was located to the south of the study grid and fence row. A 2 m high chain link fence paralleled Hagadorn and Sandhill roads, and a gate to the south of the grid provided privileged access to the study site. During the course of my research, areas adjacent to the study site were used in other experiments by members of Michigan State University's Departments of Botany and Zoology.

Abundant small mammals at the study site included Microtus pennsylvanicus, Zapus hudsonicus, and Blarina brevicauda. Less abundant species included Peromyscus leucopus, Scalopus aquaticus, Sorex cinereus, Marmota monax, Procyon lotor, Mustela nivalis, and Mustela frenata. Occurring rarely were Felis domestica and Vulpes vulpes. Four species of snakes were found at the study site; these included Thamnophis sirtalis sirtalis, Thamnophis butleri, Lampropeltis triangulum triangulum, and Storeria dekayi dekayi.

Trapping records from a study preceding this one at the same site (King, 1983) revealed that P. m. bairdi were probably not originally present. This study site does not offer the most favorable P. m. bairdi habitat (King, 1983). In the mid-Michigan area this subspecies is most commonly found in or near disturbed agricultural fields of

alfalfa, corn, oats, wheat or clover (J. King, pers. comm.; Linduska, 1950). The nearest agricultural field to the study site was an isolated corn field located approximately 2 km to the northeast. Nevertheless, trapping records kept since the completion of King's study and prior to the beginning of the present research revealed the presence of some indigenous P. m. bairdi. These mice, however, were probably the wild-born descendants of experimental mice introduced in earlier experiments.

As part of the general scheme to provide experimental control of available nest sites, food, water, and refuges from predators, the study site was provided with microhabitats that were proven to be favorable to the mice (King, 1983). The microhabitat enclosures consisted of 32 cylinders arranged in pairs, with 16 pairs forming a square grid, 120 m on a side (Figure 3.1). Each pair of cylinders was spaced 40 m apart. The cylinders (hereafter called arenas) were constructed from 3.2 mm sheet aluminum. Each arena was 2 m in diameter and 100 cm high. The bottom of each arena was buried 15 cm below the ground surface (Figure 3.2) to discourage burrowing animals from gaining entry to the arenas. Two arenas were spaced 2 m apart to form a pair (hereafter called a couplet). Each arena was provided with four shelters constructed from concrete building blocks (20 cm x 20 cm x 40 cm) and concrete patio blocks (5 cm x 20 cm x 40 cm). Access passageways into and between the three chambers of each building block (hereafter called a nest) were provided by cutting 2.5 cm x 2.5 cm square notches (Figure 3.2). A concrete patio block was placed at the top and bottom of each nest. A 30 cm x 50 cm plywood roof, waterproofed with marine varnish, was placed between the

top of the nest and the patio block to provide extra insulation and waterproofing for the nest below. The four nests were placed strategically within each arena to provide mice with a diversity of available microhabitats. Two of the nests were placed at ground level on opposite sides within the circular arena, one was buried so that its roof was at ground level, and the fourth was placed upon a building block laying on its side in the center of the arena (Figure 3.2). Thus, each arena had one subterranean, one elevated, and two surface-level nests. A small 2.5 cm diameter exit hole, located 20 cm high on the arena wall, allowed passage of mice into and out of the arena. One of the surface nests was placed directly beneath the exit hole and an additional surface nest was placed outside of the arena wall beneath the hole (Figure 3.2). Peromyscus m. bairdi readily climb the surface nests and easily locate the exit hole. The height of the exit hole served as a deterrent to arena entry by more-terrestrial vertebrates such as M. pennsylvanicus, B. brevicauda, S. cinereus, and snakes.

Each arena was provisioned with supplemental food, water, and nesting material. Unshelled sunflower seeds were added on a regular basis to one of the surface nests in each arena (Figure 3.2) and to additional surface nests placed halfway (20 m) between couplets. A second surface nest and the subterranean nest received compressed cotton nesting material (Nestlets, Ancare Corp.). Fresh Nestlets were added to these nests on a regular basis as needed during the course of the experiments. Supplemental water was provided during seasonal dry periods. Periodic maintenance at the arenas included trimming weeds and grasses when they obstructed the nests, realigning displaced

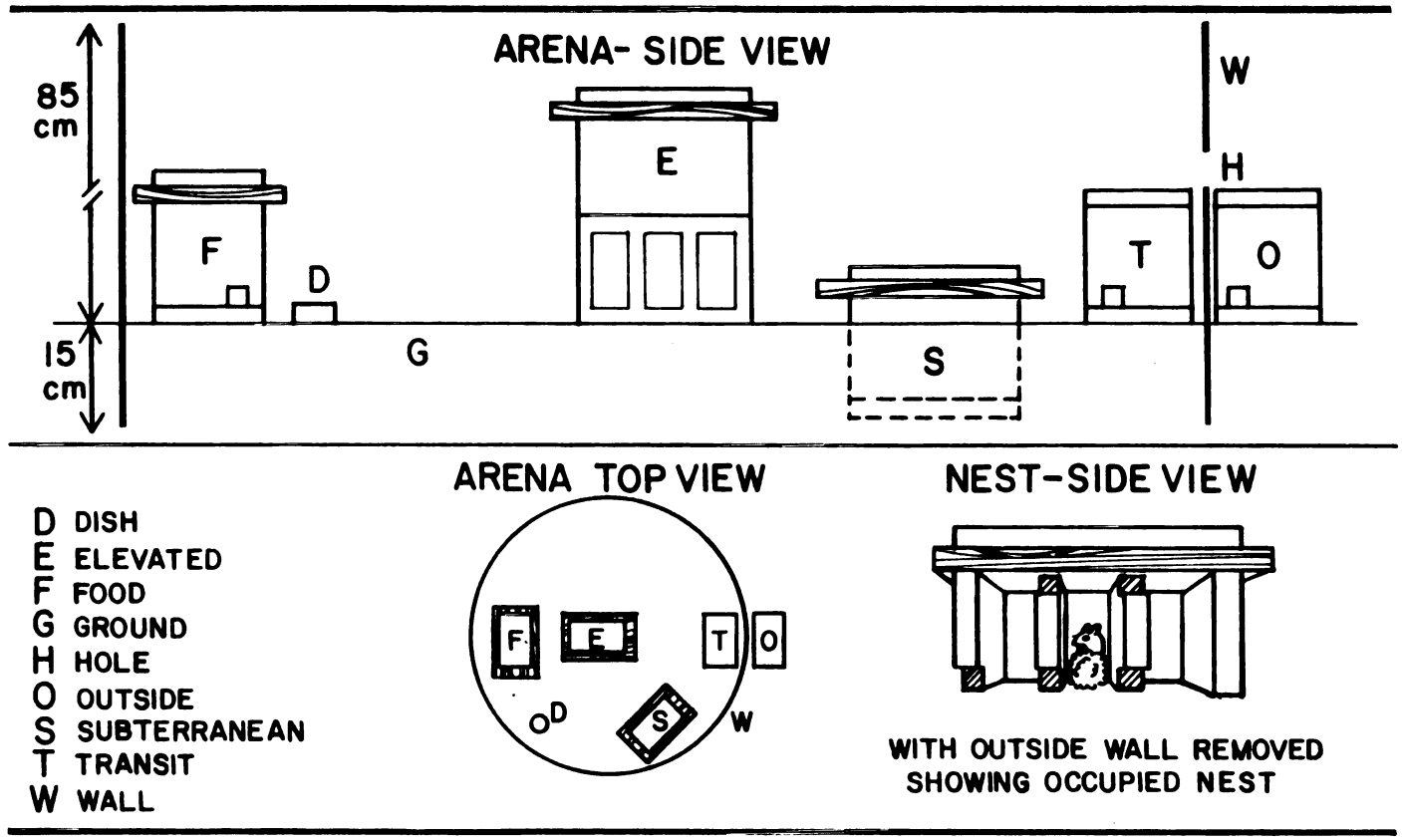


Figure 3.2 Schematic diagrams of an arena and a nest-box.

nest blocks, and cleaning debris from within the occupied or abandoned nests. In spite of the buried walls, S. aquaticus occasionally tunneled underneath the arena walls which caused concern that mice might take refuge inside tunnels. When Scalopus tunnels were observed they were destroyed. Eight of the 32 arenas received a subterranean floor fashioned from 6.4 mm mesh hardware cloth. This mesh floor effectively prevented burrowing animals from gaining entry into these arenas. To facilitate the inter-couplet movement of mice, eight 2 m-wide paths (four in the east-west direction and four in the north-south direction) were provided by periodically mowing the vegetation to a height of approximately 10 cm. This operation was performed prior to the beginning of the experiments.

Mice were introduced into the microhabitat study site (hereafter called mouse cities) at the beginning of each four experimental seasons by using procedures described by King (1983). Each experimental population was started by introducing eight bisexual, mated adult pairs of P. m. bairdi into the mouse cities. The mice used were trapped from agricultural fields in the vicinity of Michigan State University at least one month prior to the start of each experiment and brought into the mouse breeding colony at the University. Bisexual mated pairs were immediately established and housed in 13 cm x 28 cm x 40 cm deep plastic cages. Each cage contained wood shavings, nesting material (Nestlets, Ancare Corp.) and ad libitum food (Wayne Breeder Blox), and water. Diet was supplemented with unshelled sunflower seeds. The room temperature in the breeding colony was maintained at approximately 23^{o}C, and the mice were exposed to 15 hours of white fluorescent light and nine hours of darkness per

day (15L:9D). All field-conceived litters were discarded at weaning due to paternal uncertainty. When a female was conspicuously pregnant by her current mate, she and her mate were introduced into a nest in the north arena of one of eight introductory couplets (Figure 3.3).

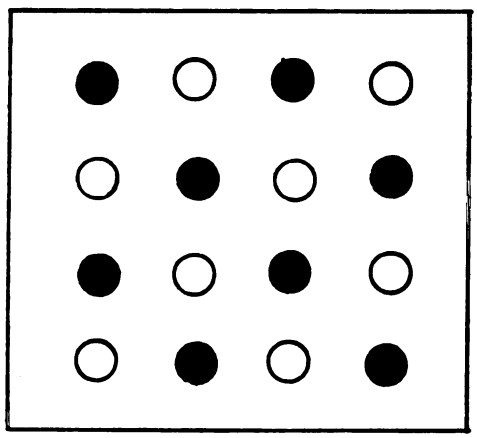


Figure 3.3 Pattern of introduction of breeding pairs to couplets at the mouse cities. Darkened circles represent introductory couplets.

This process continued until the eight mated pairs occupied nests in eight different couplets. An attempt was made to synchronize the introduction dates of all bisexual pairs to within seven to ten days of each other. This was more successful in some seasons than in others (Table 3.1.).

Table 3.1 Introduction dates of the original bisexual pairs.

Season			
Summer 1981	Fall 1981	Spring 1982	Summer 1982
7-7	9-26	4-8	7-2
7-7	9-26*	4-8	7-2
7-7	9-26*	4-8	7-3
7-11	9-26*	4-8	7-9
7-13	10-2*	4-10	7-12
7-16	10-7*	4-11	7-12
7-18	10-7	4-11	7-15
7-19	10-12	4-14	7-15

*Replaced on 11-2, 11-2, 11-3, 11-3, 11-4, 11-5; see text for explanation.

The mice were confined to their home arena upon introduction by blocking the arena's exit hole. After a ten-day familiarization period, the exit holes were opened and mice were free to move about the study site. In some seasons from an earlier study (King, 1983), one or both members of certain introduced pairs either disappeared or died during the familiarization period. In anticipation of this problem, extra bisexual pairs were introduced as "stand-bys" into the south arena of the introductory couplets. If any problem occurred with the pair introduced to the north arena, these mice were removed and the bisexual pair in the south arena became the designated family for that particular couplet. A serious problem occurred in the Fall 1981 experiment with five bisexual pairs and their litters were killed by at least two Mustela nivalis after the experiment was three weeks old. Six bisexual pairs left in the breeding colony as stand-bys were introduced as replacements (Table 3.1).

Each seasonal experiment began on the date that the first bisexual pair was introduced and continued for approximately ten weeks. On every third day, all nests were carefully examined and the presence of the mice recorded. Mice found in the nests were removed with long-handled, rubber-tipped forceps and identified from a numbered tag in each ear (size 1 Monel fingerling tags, National Band and Tag). Mice born in the mouse cities were ear-tagged at 18-21 days of age. Ear tags were replaced when lost, and although mice occasionally lost ear tags, they rarely lost both. Thus, the only unknown mice were those that were never tagged. In addition to recording the tag numbers, the following data were collected: 1) nest location, 2) body weight to the nearest 0.5 g (measured on a Pesola spring scale (Bleitz Wildlife)), 3) sex, and 4) reproductive status (for males, position of the testes - scrotal or abdominal; for females, condition of the vagina - perforate or imperforate, and pregnancy or lactation). New litters were noted and carefully examined to estimate the date of birth ($\pm$1 day). Pigmentation of the dorsum and the erection of the pinnae of the neonates were used as an aid in determining birth dates. The adult females of the introduced pairs all gave birth to their first, field-born litters within ten days of introduction to the mouse cities. Thus, all first-born litters in each season were born within two weeks of each other.

Notes were taken regarding any unusual observations such as wounding, parasitism, deaths, and instances of cohabitation by other mammal species. After attending to all of the nests, four traplines containing a total of 83 small-mammal live-traps (L. M. Leathers and Sons) were baited with sunflower seeds and set (Figure 3.1). During

periods of cool weather, Nestlets were added to the traps prior to being set. Three of the traplines were located 100 m to the north, south, and west of the study grid. These traplines described above were spaced at 10 m intervals. A fourth trapline containing 20 traps placed at 20 m intervals was established on the perimeter of the study grid. This perimeter trapline was separated from the outer boundary of the couplets by 20 m. Records of the numbers of each species captured were made and any tagged P. m. bairdi were identified and released.

Juveniles born during the Summer 1981, Spring 1982, and Summer 1982 seasons served as the experimental subjects which received either a melatonin or control implant on the day they were tagged (see Materials and Methods for Experiment 3.1 below). Weanling mice in the Fall 1981 experiment received either a steroid or control implant (see Materials and Methods for Experiment 3.2 below).

EXPERIMENT 3.1: SPRING AND SUMMER DISPERSAL IN JUVENILES: EFFECTS OF DELAYING GONADAL MATURATION

The general hypothesis tested in this experiment is that an experimentally induced delay in the gonadal maturation of juvenile P. m. bairdi will either prevent or delay their dispersal.

Materials and Methods

On the day of tagging, male and female juveniles from each litter randomly received either a melatonin or control implant. Whenever possible, I attempted to apply the treatments equally by sex within each litter. The methods for preparing and injecting the implants were described in Chapter Two. When subsequent nest-box checks revealed the presence of implant-treated mice, I palpated the skin

above the scapular region of each mouse to confirm the presence of the implant. None of the treated mice lost their implants during the course of the study.

Analysis

The following hypotheses pertain to the general prediction that melatonin treatment will cause a delay in gonadal maturation in juvenile P. m. bairdi. I could not sacrifice experimental animals to surgically assess the antigonadal effectiveness of the treatments as I did in previous laboratory tests (Chapter Two); instead, I used age at puberty (measured as the age at first observation of palpable or scrotal testes in males or perforate vagina in females) to estimate the age of gonadal maturity.

1. Probability of ultimate attainment of puberty by juveniles in the population is independent of treatment (melatonin or control implant).
2. Melatonin-treated individuals will reach puberty at an older age than control-treated individuals.
3. Melatonin-treated individuals will weight more at puberty than control-treated individuals.

A further prediction regarding gonadal maturation concerns the likelihood of pregnancies in first-born, treated females. I predicted that melatonin-treated females are less likely to become pregnant than control-treated females.

The remaining hypotheses refer to the general prediction that dispersal will be prevented or postponed in juveniles treated with melatonin. Dispersal is operationally defined here in two ways: 1) resident, inter-couplet movement away from the natal couplet (at least

one inter-couplet movement), and 2) permanent disappearance from the study site. For any given individual, the age at dispersal is measured as the age of the individual at its last known occupance in a nest-box prior to permanent disappearance from the study site.

1. Melatonin-treated individuals are less likely to disappear from the population than control-treated individuals.
2. Melatonin-treated individuals will disappear from the population at an older age than control-treated individuals.
3. Melatonin-treated individuals will weigh more at disappearance than will control-treated individuals.
4. Resident, melatonin-treated individuals are less likely to make inter-couplet movement than resident, control-treated individuals.
5. Melatonin-treated mice are less likely to be captured in peripheral or perimeter traplines than control-treated mice.

An important prediction is that disappearing mice are more likely to be pubertal than non-pubertal. Furthermore, I predicted that a positive relationship exists between age at puberty and age at disappearance. I also predict that weight of individuals at puberty will be positively associated with weight of individuals at disappearance.

Various parametric statistical tests were used to analyze data: Chi-square tests of independence (X^2), t-tests (t, t' (approximate t- used when variances are unequal)), analyses of variance (one-way, factorial and mixed-classification), and simple linear regression (r^2).

Most, but not all, of the introduced adult females gave birth to two or more litters during the ten-week experiments. Based on laboratory evidence from the literature which shows that litter order can affect litter size (Drickamer and Vestal, 1973; Myers and Master, 1983), I chose to include parity as an independent variable in all of the analyses. Only mice from first and second litters were used in the analyses because few mothers gave birth to a third litter, and for those which did, the third litter offspring were not old enough to receive treatment prior to the end of the ten-week experiment.

There were two separate analyses of variance on each of the dependent variables (age and weight of juveniles at puberty; age and weight of juveniles at disappearance). The first, a mixed-classification ANOVA, served to examine whether there was an effect of mother within season (random effect), or litter order (fixed effect) on the dependent variable in question.

In the preliminary mixed-classification ANOVA, only data from offspring of mothers that gave birth to two litters during the experiment were used. A maximum likelihood method of analysis was used due to the mixed effect model and unbalanced cells in the statistical design. These mixed-effect ANOVAS were performed with the aid of a BMD (Department of Biomathematics, University of California) computer program (BMDP3V - General Mixed Model Analysis of Variance - Restricted Maximum Likelihood Method) which was run on Michigan State University's CDC-6000 computer. It should be noted here that this program does not provide a direct output of the estimated mean squares for random effects (in this case, mother within season). Nonetheless, I estimated components of variance for the random effects by deriving

the expectations of the mean squares (C. Anderson, pers. comm.; Gill, 1978; Satterthwaite, 1941). Thus, the reported probabilities (Tables 3, 5, 9, 11) of Type I error due to the random effect of mother within season are not exact, but obtained from available statistical tables (e.g. Gill, 1978).

If mother within season had no effect on each dependent variable, I dropped this factor from the model and reanalyzed the data according to a four-way (treatment, sex, season, and litter order (includes litters from all adult females, including those females which only had one litter)) fixed-effect ANOVA. Furthermore, if any main effect or interaction of main effects was negligible (i.e. had probability of Type I error $p > 0.275$ (C. Anderson; pers. comm.)), these factors were pooled with experimental error to gain degrees of freedom for testing the remaining effects. Due to the unbalanced data, reduction in sums of squares were calculated to provide the most conservative estimate of the sums of squares due to any main effect (Speed and Hocking, 1976). Factorial and one-way ANOVAS were conducted with the aid of SPSS computer programs (ONE-WAY and MANOVA).

Linear regression plots were made with the assistance of an SPSS plotting program called PLOT. T-tests were performed with the aid of the SPSS program called T-TEST.

Results

Effects of Treatments on Attainment of Puberty

The null hypothesis that attainment of puberty is independent of treatment could not be rejected ($X^2 = 0.61$; $df = 1$; $p > 0.60$; Table 3.2a).

Table 3.2a Frequencies with which melatonin- and control-treated juveniles (at least 30 days old) became pubertal or remained non-pubertal.

	Treatment (Sexes, Seasons Pooled)	
Response	Melatonin	Control
Pubertal	68	68
Non-Pubertal	34	26
Totals	N=102	N=94

$X^2 = 0.61$, df = 1, $p > 0.60$

Melatonin-treated mice, present in the population for at least 30 days, were as likely to become pubertal as controls that were present in the population for a comparable length of time. Further tests of the independence of the primary criterion of interest, attainment of puberty, and the secondary criteria of season (Summer 1981, Spring 1982, and Summer 1982) and sex were performed. The acceptance or rejection of the null hypotheses is based on two-tailed chi-square tests. Puberty was found to be independent of sex ($X^2 = 0.001$; df = 1; $p > 0.06$; Table 3.2b), but not season ($X^2 = 11.13$; df = 2; $p < 0.01$; Table 3.2c). A significantly greater percentage of mice became

Table 3.2b Frequencies with which males and females became pubertal or remained non-pubertal.

Sex (Treatments, Seasons Pooled)		
Response	Male	Female
Pubertal	66	70
Non-Pubertal	29	31
Totals	N=95	N=101

$X^2 = 0.001$, df = 1, $p > 0.60$

Table 3.2c Frequencies with which individuals in each season became pubertal or remained non-pubertal.

Season (Treatments, Sexes Pooled)			
Response	Summer 1981	Spring 1982	Summer 1982
Pubertal	29	71	36
Non-Pubertal	17	16	27
Totals	N=46	N=87	N=63

$X^2 = 11.13$, df = 2, $p < 0.01$

pubertal in the spring season than summer. Following procedures outlined by Gill (1978), I conducted further tests involving two-way combinations of treatment, season, and sex in an attempt to discover any dependencies among the secondary criteria as they affected the attainment of puberty. The results of these tests (Table 3.2d-e) reveal that, regardless of treatment, male mice in the spring season were more likely to become pubertal than males in either of the summer seasons.

Although melatonin treatment had no effect on the number of mice which attained puberty relative to control-treated mice, melatonin-treated individuals reached puberty at an older age than controls as predicted ($F = 34.400$; $df = 1/113$; $p < 0.001$; Table 3.3, Figure 3.4).

Table 3.3 Analysis of variance of age at puberty.

	Analysis of Variance			
Source of Variance	DF	MS	F	PROB
Treatment	1	2033.746	34.401	$p < 0.001$
Sex	1	167.966	2.840	NS
Season X Treatment	2	146.392	2.476	NS
Season X Treatment X Litter	2	202.694	3.428	$p < 0.05$
Error	113	59.118		
Total	119			

There was also, however, a significant three-way interaction of treatment by season by litter order ($F = 3.428$; $df = 2/113$; $p < 0.05$; Table 3.3). Melatonin-treated individuals from the first-born litters in all seasons reached puberty later than controls. In both summer seasons, however, the age that second-litter mice reached puberty was

Table 3.2d **Frequencies with which males and females (for each season) became pubertal or remained non-pubertal.**

Sex (Treatments Pooled)

	Males			Females		
Response	Summer 1981	Spring 1982	Summer 1982	Summer 1981	Spring 1982	Summer 1982
Pubertal	11	39	16	18	32	20
Non-Pubertal	9	8	12	8	8	15
Totals	N=20	N=47	N=28	N=26	N=40	N=35

$X^2 = 8.05$, df = 2, $p < 0.05$ (Males)

$X^2 = 4.63$, df = 2, $p > 0.20$ (Females)

Between Season Comparison (Males)

Spring 1982 vs. Summer 1982 $X^2_B = 5.98$, df = 1, m = 3, $p < 0.05$

Spring 1982 vs. Summer 1981 $X^2_B = 5.80$, df = 1, m = 3, $p < 0.05$

Summer 1981 vs. Summer 1982 $X^2_B = 0.02$, df = 1, m = 3, $p > 0.05$

Table 3.2e **Frequencies with which melatonin- and control-treated juveniles (for each season) became pubertal.**

	Treatment (Sexes Pooled)					
	Melatonin			Control		
Response	Summer 1981	Spring 1982	Summer 1982	Summer 1981	Spring 1982	Summer 1982
Pubertal	14	36	18	15	35	18
Non-Pubertal	11	10	13	6	6	14
Totals	N=25	N=46	N=31	N=21	N=41	N=32
	$X^2 = 5.10$, df = 2, $p > 0.10$			$X^2 = 7.03$, df = 2, $p > 0.05$		

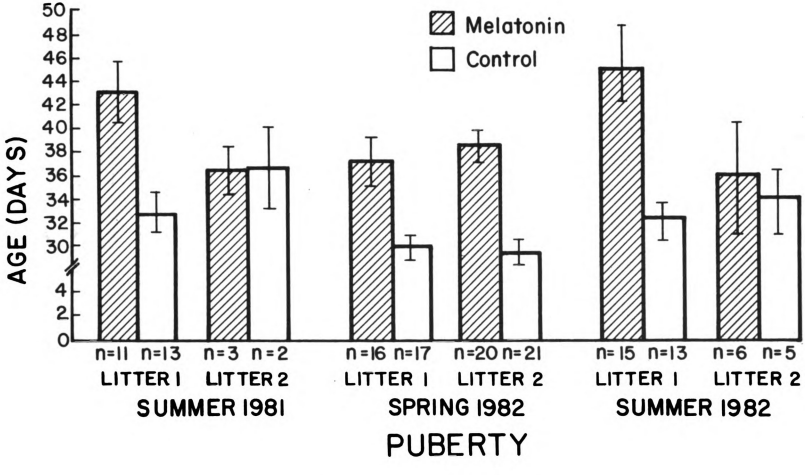


Figure 3.4 Mean age at puberty. Vertical lines indicate $\pm$ 1 S.E.

only slightly greater for melatonin-treated individuals than controls. The preliminary, mixed effect ANOVA revealed no significant effect of mother on the age that mice attained puberty (Table 3.4).

Table 3.4 Preliminary mixed-effect analysis of variance of age at puberty.

	Analysis of Variance			
Source of Variance	DF	MS	F	PROB
Treatment	1	32.18	1.25	0.267
Sex	1	37.32	1.45	0.232
Litter	1	13.13	0.51	0.476
Season	2	10.04	0.39	0.676
Treatment X Sex	1	6.18	0.24	0.629
Treatment X Season	2	59.46	2.31	0.106
Treatment X Litter	1	0.51	0.02	0.881
Sex X Litter	1	3.35	0.13	0.720
Sex X Season	2	7.72	0.30	0.739
Litter X Season	2	9.27	0.36	0.701
Treatment X Litter X Season	2	71.81	2.79	0.068
Treatment X Sex X Season	2	0.02	0.00	0.999
Treatment X Sex X Litter	1	1.80	0.07	0.796
Sex X Litter X Season	2	0.26	0.01	0.989
Sea X Trt X Lit X Sex	2	0.77	0.03	0.967
Mother Within Season	18	4.89	0.19	$p > 0.50$
Error	75	25.74		

As expected, melatonin-treated mice weighed more at puberty than controls ($F = 17.809$; $df = 1/118$; $p < 0.001$; Table 3.5, Figure 3.5). Furthermore, there was a significant interaction of season by sex ($F = 3.556$; $df = 2/118$; $p < 0.05$; Table 3.5), with males from the spring season consistently weighing more at puberty than females. As was the case for age at puberty, there was no significant effect of mother on the weights of mice at puberty (Table 3.6).

Table 3.5 Analysis of variance of weight at puberty.

Source of Variance	Analysis of Variance DF	MS	F	PROB
Treatment	1	47.801	17.809	$p < 0.001$
Treatment X Sex	1	2.692	1.002	NS
Season X Sex	2	9.545	3.556	$p < 0.05$
Season X Treatment X Litter	2	6.952	2.590	NS
Error	112	2.684		
Total	118			

Table 3.6 Preliminary mixed-effect analysis of variance of weight at puberty.

Source of Variance	Analysis of Variance DF	MS	F	PROB
Treatment	1	5.36	2.33	0.104
Sex	1	1.10	0.48	0.490
Litter	1	0.55	0.24	0.627
Season	2	0.76	0.33	0.719
Treatment X Sex	1	3.73	1.62	0.206
Treatment X Season	2	0.01	0.00	0.998
Treatment X Litter	1	0.01	0.00	0.998
Sex X Litter	1	0.21	0.09	0.766
Sex X Season	2	14.49	6.30	0.003
Litter X Season	2	0.44	0.19	0.824
Treatment X Litter X Season	2	5.27	2.29	0.108
Treatment X Sex X Season	2	0.32	0.14	0.870
Treatment X Sex X Litter	1	0.07	0.03	0.859
Sex X Litter X Season	2	1.17	0.51	0.603
Sea X Trt X Lit X Sex	2	0.51	0.22	0.800
Mother Within Season	18	0.05	0.02	$p > 0.50$
Error	75	2.30		

As predicted, melatonin-treated females were less likely to become pregnant than control females (one-tailed $X^2 = 5.73$; df = 1; $p < 0.025$; Table 3.7). Fifty-seven percent of the control females

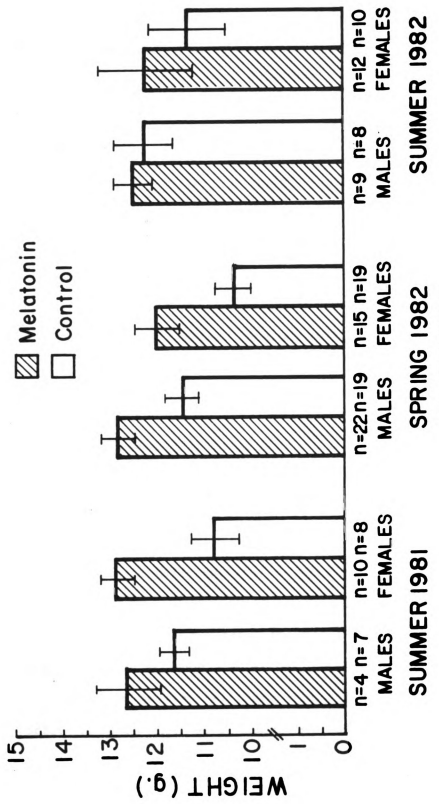


Figure 3.5 Mean weight at puberty. Vertical lines indicate ± 1 S.E.

Table 3.7 Frequencies with which melatonin- and control-treated females (at least 50 days old) became pregnant.

	Treatment (Seasons Pooled)	
Responses	Melatonin	Control
Pregnant	3	8
Not Pregnant	15	6
Totals	N=18	N=14

*X^2 = 5.73, df = 1, $p < 0.025$

*one-tailed

(at least 50 days old, an age at which first pregnancies can be visibly detected) became pregnant compared with only 17% of the melatonin-treated females. Seasons were pooled in the above analysis due to the small number of females that became pregnant in each season.

Effects of Treatment on Dispersal

In all of the populations studied there was a continuum in the length of residency for the mice. I chose to distinguish between mice that disappeared from the population and those that stayed. These two categories were differentiated on the basis of whether residency was less than or greater than the median length of occupancy (in days) for all treated mice. In other words, individuals which remained in the population for at least the median length of occupancy (42 days) were considered to be stayers. Mice that disappeared from the population prior to this time were classified as mice that disappeared. As predicted, melatonin-treated individuals were less likely to disappear than controls (one-tailed $X^2 = 39.03$; df = 1; $p < 0.001$; Table 3.8a).

Table 3.8a Frequencies with which melatonin- and control-treated juveniles disappeared from the population or stayed.

	Treatment (Sexes, Seasons Pooled)	
Response	Melatonin	Control
Stay*	72	29
Disappear	33	82
Totals	N=105	N=111

**X^2 = 39.03, df = 1, p < 0.001

*Individuals who remained in population until at least the median age of occupancy for all treated mice (42 days)

**One-tailed

I performed additional tests to determine the degree of independence of residency (stay or disappear) from the secondary criteria of interests - season and sex. The acceptance or rejection of the null hypotheses is based on two-tailed chi-square tests. Length of residence was independent of sex (X^2 = 0.72; df = 1; p > 0.60; Table 3.8c) but not season (X^2 = 21.20; df = 2; p < 0.001; Table 3.8b).

Table 3.8b Frequencies with which individuals in each season disappeared from the population or stayed

	Season (Treatments, Sexes, Pooled)		
Response	Summer 1981	Spring 1982	Summer 1982
Stay	27	30	44
Disappear	19	70	26
Totals	N=46	N=100	N=70

X^2 = 21.2, df = 2, p < 0.001

Table 3.8c Frequencies with which males and females disappeared from the population or stayed.

	Sex (Treatments, Seasons Pooled)	
Response	Male	Female
Stay	46	55
Disappear	59	56
Totals	105	111

$X^2 = 0.72$, df = 1, $p > 0.60$

Significantly more mice disappeared from the spring population than expected. Tests involving two-way combinations of treatment, season, and sex revealed that control mice (for each sex and in each season) were more likely to disappear than melatonin-treated individuals (Table 3.8d-e). Similarly, spring mice (for each sex and treatment)

Table 3.8d Frequencies with which males and females (for ech treatment) disappeared from the population or stayed.

	Sex (Seasons Pooled)			
	Male		Female	
Response	Melatonin	Control	Melatonin	Control
Stay	35	11	34	20
Disappear	18	41	15	41
Totals	N=53	N=52	N=49	N=62
	$X^2 = 21.54$, df = 1, $p < 0.001$		$X^2 = 14.54$, df = 1, $p < 0.001$	

Table 3.8e Frequencies with which individuals in each season (for each treatment) disappeared from the population or stayed.

	Season (Sexes Pooled)					
	Summer 1981		Spring 1982		Summer 1982	
Response	Melatonin	Control	Melatonin	Control	Melatonin	Control
Stay	19	8	25	5	28	16
Disappear	4	15	23	47	6	20
Totals	N=23	N=23	N=48	N=52	N=34	N=36
	$X^2 = 10.02$, df = 1, $p < 0.01$		$X^2 = 19.54$, df = 1, $p < 0.001$		$X^2 = 11.46$, df = 1, $p < 0.005$	

were more likely to disappear than mice from either summer season (Table 3.8f-g).

In addition to disappearing from the population with less frequency than controls, melatonin-treated mice disappeared at an older age ($F = 34.759$; df = 1/161; $p < 0.001$; Table 3.9, Figure 3.6).

Table 3.9 Analysis of variance of age at disappearance.

	Analysis of Variance			
Source of Variance	DF	MS	F	PROB
Treatment	1	3824.511	34.759	$p < 0.001$
Sex	1	309.363	2.812	NS
Litter	1	0.148	0.001	NS
Season	2	698.767	6.351	$p < 0.005$
Sex X Treatment	1	4.920	0.045	NS
Error	161	110.029		
Total	167			

Table 3.8f **Frequencies with which males and females (for each season) disappeared from the population or stayed.**

	Sex (Treatments Pooled)					
	Male			Female		
Response	Summer 1981	Spring 1982	Summer 1982	Summer 1981	Spring 1982	Summer 1982
Stay	13	15	12	14	15	26
Disappear	7	40	18	12	30	14
Totals	N=20	N=55	N=30	N=26	N=45	N=40

$X^2 = 13.02$, df = 2, $p < 0.01$ $\quad$ $X^2 = 8.76$, df = 2, $p < 0.05$

Between Season Comparisons (Males):

Spring 1982 vs. Summer 1981 $X^2_B = 5.98$, df = 1, m = 3, $p < 0.05$

Spring 1982 vs. Summer 1982 $X^2_B = 5.80$, df = 1, m = 3, $p < 0.05$

Summer 1981 vs. Summer 1982 $X^2_B = 0.02$, df = 1, m = 3, $p > 0.05$

Between Season Comparisons (Females):

Spring 1982 vs. Summer 1982 $X^2_B = 8.49$, df = 1, m = 3, $p < 0.05$

Spring 1982 vs. Summer 1981 $X^2_B = 2.90$, df = 1, m = 3, $p > 0.05$

Summer 1981 vs. Summer 1982 $X^2_B = 0.34$, df = 1, m = 3, $p > 0.05$

Table 3.8g Frequencies with which melatonin- or control-treated juveniles (for each season) diseappeared from the population or stayed.

	Treatment (Sexes Pooled)					
	Melatonin			Control		
Response	Summer 1981	Spring 1982	Summer 1982	Summer 1981	Spring 1982	Summer 1982
Stay	19	25	28	8	5	16
Disappear	4	23	6	15	47	20
Totals	N=23	N=48	N=34	N=23	N=52	N=36
	$X^2 = 11.17$, df = 2, $p < 0.01$			$X^2 = 14.51$, df = 2, $p < 0.005$		

Between Seasons Comparisons (Melatonin):

Spring 1982 vs. Summer 1981 $X^2_B = 6.16$, df = 1, m = 3, $p < 0.05$

Spring 1982 vs. Summer 1982 $X^2_B = 7.97$, df = 1, m = 3, $p < 0.05$

Summer 1981 vs. Summer 1982 $X^2_B = 0.01$, df = 1, m = 3, $p > 0.05$

Between Seasons Comparisons (Control):

Spring 1982 vs. Summer 1981 $X^2_B = 7.03$, df = 1, m = 3, $p < 0.05$

Spring 1982 vs. Summer 1982 $X^2_B = 14.19$, df = 1, m = 3, $p < 0.01$

Summer 1981 vs. Summer 1982 $X^2_B = 0.55$, df = 1, m = 3, $p > 0.05$

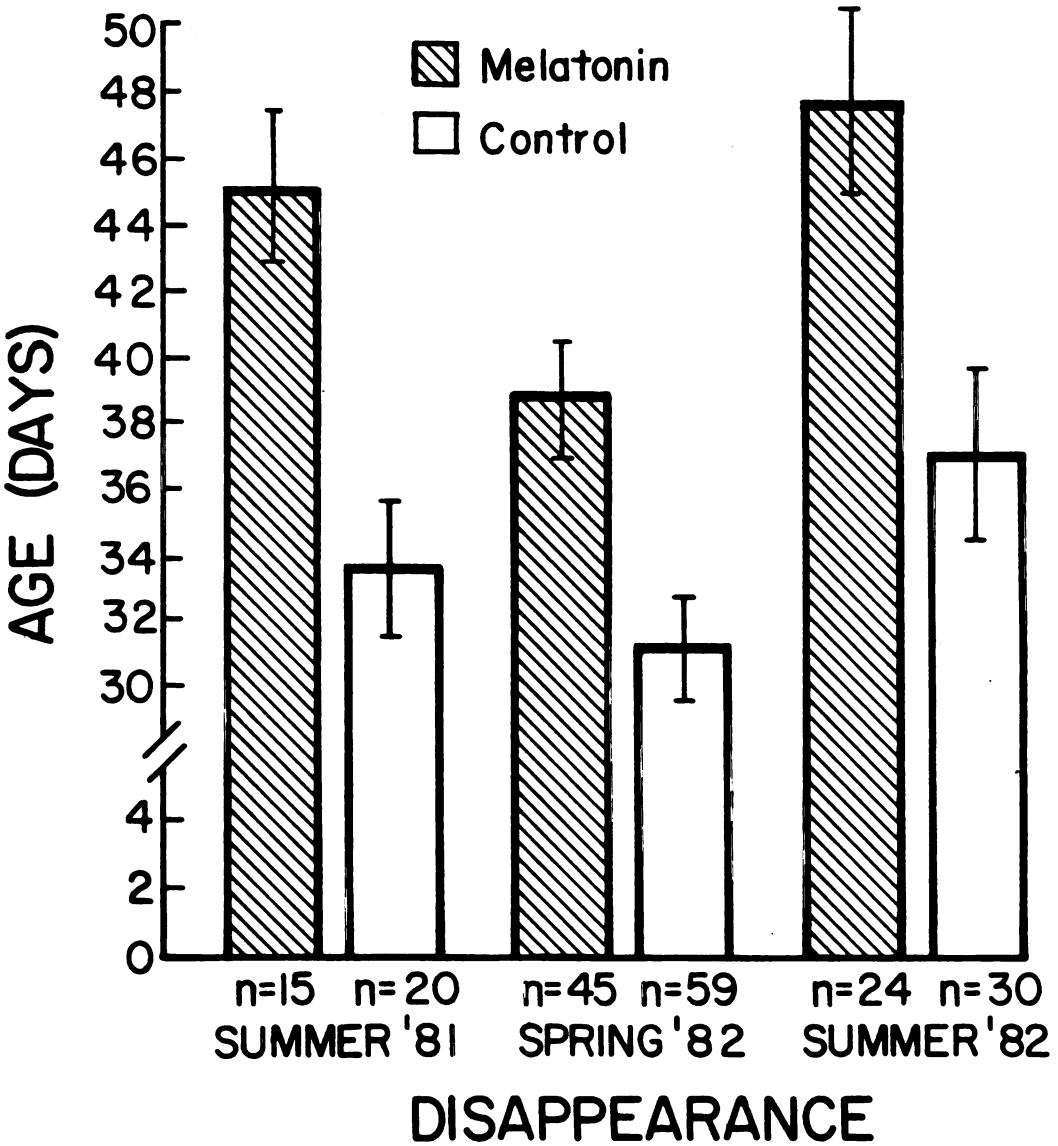


Figure 3.6 Mean age at disappearance. Vertical lines indicate $\pm$ 1 S.E.

Furthermore, there was a significant effect due to season ($F = 6.351$; $df = 2/161$; $p < 0.005$; Table 3.9). Regardless of treatment, mice from the spring season disappeared at an earlier age than mice from either summer season. There was no significant effect of mother on the age at which mice disappeared (Table 3.10).

Table 3.10 Preliminary mixed-effect analysis of variance of age at disappearance.

	Analysis of Variance			
Source of Variance	DF	MS	F	PROB
Treatment	1	577.69	8.63	0.004
Sex	1	145.26	2.17	0.144
Litter	1	241.65	3.61	0.060
Season	2	109.11	1.63	0.200
Treatment X Sex	1	293.87	4.39	0.039
Treatment X Season	2	47.52	0.71	0.494
Treatment X Litter	1	16.06	0.24	0.627
Sex X Litter	1	13.39	0.20	0.657
Sex X Season	2	20.08	0.30	0.740
Litter X Season	2	37.49	0.56	0.573
Treatment X Litter X Season	2	52.21	0.78	0.461
Treatment X Sex X Season	2	10.04	0.15	0.865
Treatment X Sex X Litter	1	0.06	0.00	0.983
Sex X Litter X Season	2	42.84	0.64	0.531
Sea X Trt X Lit X Sex	2	86.35	1.29	0.279
Mother Within Season	18	11.38	0.17	$p > 0.50$
Error	109	66.94		

Melatonin-treated individuals weighed more at disappearance than controls ($F = 20.648$; $df = 1/167$; $p < 0.001$; Table 3.11, Figure 3.7). There was no significant effect of mother on the weights of disappearing mice (Table 3.12).

Table 3.11 Analysis of variance of weight at disappearance.

Source of Variance	Analysis of Variance DF	MS	F	PROB
Treatment	1	130.788	20.648	$p < 0.001$
Sex	1	22.544	3.559	NS
Season X Treatment	2	2.024	0.320	NS
Error	167	6.334		
Total	171			

Table 3.12 Preliminary mixed-effect analysis of variance of weight at disappearance.

Source of Variance	Analysis of Variance DF	MS	F	PROB
Treatment	1	14.82	2.56	0.113
Sex	1	12.68	2.19	0.142
Litter	1	2.26	0.39	0.532
Season	2	4.34	0.75	0.473
Treatment X Sex	1	3.18	0.55	0.461
Treatment X Season	2	10.71	1.85	0.162
Treatment X Litter	1	1.74	0.30	0.586
Sex X Litter	1	0.46	0.08	0.784
Sex X Season	2	0.29	0.05	0.948
Litter X Season	2	0.98	0.17	0.841
Treatment X Litter X Season	2	5.04	0.87	0.420
Treatment X Sex X Season	2	4.75	0.82	0.441
Treatment X Sex X Litter	1	0.06	0.01	0.907
Sex X Litter X Season	2	2.08	0.36	0.696
Sea X Trt X Lit X Sex	2	2.55	0.44	0.643
Mother Within Season	18	0.46	0.08	$p > 0.50$
Error	107	5.79		

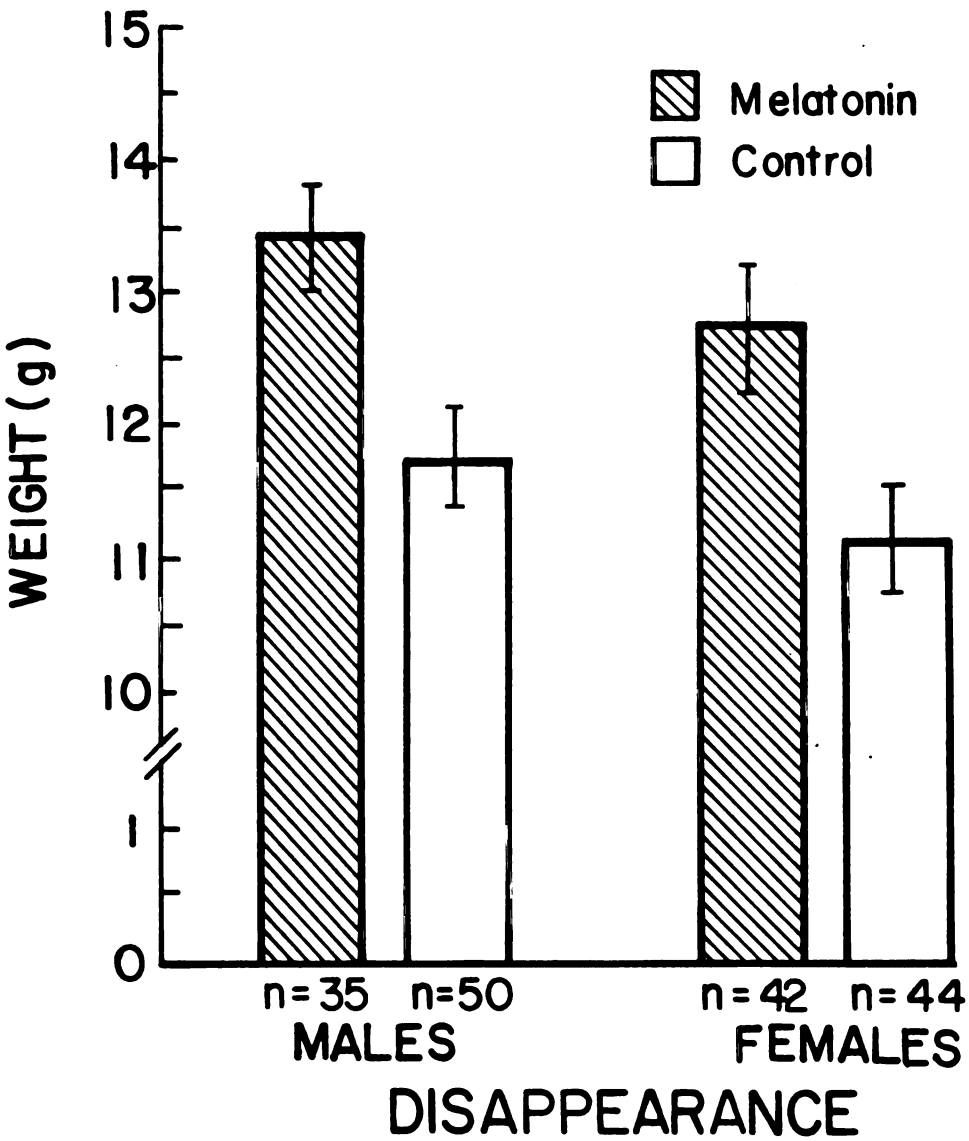


Figure 3.7 Mean weight at disappearance. Vertical lines indicate ± 1 S.E.

As an alternative measure of dispersal-related movement I assessed the rate of inter-couplet movements made by mice that did not disappear (i.e. resided in the population at least 42 days) from the population. Resident, melatonin-treated mice were less likely to make inter-couplet movements (at least one) than resident controls (one-tailed $X^2 = 8.48$; df = 1; $p < 0.005$; Table 3.13a). Again, I

Table 3.13a Numbers of melatonin- and control-treated stayers that made at least one inter-couplet movement.

	Treatment (Sexed, Seasons Pooled)	
Response	Melatonin	Control
Move	20	17
No Move	52	12
Totals	N=72	N=29

**$X^2 = 8.48$, df = 1, $p < 0.005$

*Individuals who remained in population until at least the median age of occupancy for all treated mice (42 days).
**One-tailed.

tested further to determine the degree of independence of inter-couplet movement from the secondary criteria of interest - season and sex. The acceptance or rejection of the null hypotheses is based on two-tailed chi-square tests. Inter-couplet movement was independent of both season ($X^2 = 4.23$; df = 2; $p > 0.20$; Table 3.13b) and sex ($X^2 = 0.49$, df = 1; $p > 0.60$; Table 3.13c). Although control mice were more likely to make inter-couplet movements than melatonin-treated individuals, this was only true for males (regardless of

Table 3.13b Frequencies with which stayers in each season made at least one inter-couplet movement.

	Season (Treatments, Sexed Pooled)		
Response	Summer 1981	Spring 1982	Summer 1982
Move	7	9	21
No Move	20	21	23
Totals	N=27	N=30	N=44

$X^2 = 4.23$, df = 2, $p > 0.40$

Table 3.13c Frequencies with which male and female stayers made at least one inter-couplet movement.

	Sex (Treatments, Seasons Pooled)	
Response	Male	Female
Move	17	20
No Move	29	35
Totals	N=46	N=55

$X^2 = 0.49$, df = 1, $p > 0.60$

season, Table 3.13d) and mice in the Summer 1982 season (regardless of sex, Table 3.13e).

Table 3.13d Frequencies with which male and female stayers (for each treatment) made at least one inter-couplet movement.

	Sex (Seasons Pooled)			
	Male		Female	
Response	Melatonin	Control	Melatonin	Control
Move	8	9	12	8
No Move	24	5	28	7
Totals	N=32	N=14	N=40	N=15
	$X^2 = 6.46$, df = 1, $p < 0.05$		$X^2 = 2.57$, df = 1, $p > 0.20$	

Table 3.13e Frequencies with which stayers in each season (for each treatment) made at least one inter-couplet movement.

	Season (Sexes Pooled)					
	Summer 1981		Spring 1982		Summer 1982	
Response	Melatonin	Control	Melatonin	Control	Melatonin	Control
Move	5	2	7	2	8	13
No Move	14	6	20	1	18	5
Totals	N=19	N=8	N=27	N=3	N=26	N=18
	$X^2 = 0.005$, df = 1, $p > 0.60$		$X^2 = 1.97$, df = 1, $p > 0.20$		$X^2 = 7.33$, df = 1, $p < 0.02$	

Few juveniles in any season became trapped on either the perimeter or peripheral traplines (Figure 3.1). On the peripheral traplines (100 m away from the mouse cities), three juveniles were

trapped in the Spring 1982 compared with only one in each of the summer seasons. Most trap captures of juveniles occurred on the perimeter trapline immediately surrounding (20 m away) the mouse cities. On this trapline, three juveniles were trapped in the Spring 1982 compared with seven in the Summer 1982 and none in the Summer 1981. For all seasons combined, the trap-captured mice were a random subset of the trappable population with regard to their sex, reproductive condition and hormone treatment.

Relationships Between Attainment of Puberty and Dispersal

I found that mice were more likely than not to be pubertal at their last known residency in the population (one-tailed $X^2 = 18.36$; $df = 1$; $p < 0.001$; Table 3.14a). Mice that disappeared were nearly

Table 3.14a Frequency with which individuals were pubertal at disappearance.

Responses	Observed	Expected
Pubertal	117	88.5
Non-Pubertal	60	88.5
Totals	177	177

$X^2 = 18.36$, $df = 1$, $p < 0.001$

two times more likely to be pubertal than non-pubertal. Furthermore, pubertal status was independent of treatment ($X^2 = 0.004$; $df = 1$; $p > 0.60$; Table 3.14b), season ($X^2 = 4.01$; $df = 1$; $p > 0.05$; Table 3.14c), and sex ($X^2 = 0.14$; $df = 1$; $p > 0.60$; Table 3.14d).

Table 3.14b Frequencies with which melatonin- and control-treated juveniles were pubertal at disappearance (regardless of age).

	Treatment (Sexes, Persons Pooled)	
Response	Melatonin	Control
Pubertal	57	60
Non-Pubertal	29	31
Totals	N=86	N=91

$X^2 = 0.004$, df = 1, $p > 0.60$

Table 3.14c Frequencies with which individuals in each season were pubertal at disappearance (regardless of age).

	Seasons (Treatments, Sexes Pooled)		
Response	Summer 1981	Spring 1982	Summer 1982
Pubertal	23	67	27
Non-Pubertal	11	27	22
Totals	N=34	N=94	N=49

$X^2 = 4.01$, df = 1, $p > 0.05$

Table 3.14d Frequencies with which males and females were pubertal at disappearance (regardless of age).

	Sex (Treatments, Seasons Pooled)	
Response	Male	Female
Pubertal	58	59
Non-Pubertal	28	32
Totals	N=86	N=91

$X^2 = 0.14$, df = 1, $p > 0.60$

Regression analyses of age and weight at disappearance on age and weight at puberty were performed on melatonin-treated mice and controls in each season. I conducted separate regression analyses for each season because seasonal effects on age at disappearance, age at puberty, (as in season x treatment x litter order effect), and weight at puberty (as in season x sex effect) were discovered in earlier analyses of variance (above). Only mice which became pubertal prior to disappearance could be included in the analyses. To determine whether the responses of mice used in the regression analyses were representative of all other treated mice (including mice which disappeared prior to reaching puberty, and mice which failed to disappear after reaching puberty but prior to the completion of the experiment), I used t-tests to compare the ages and weights at puberty and disappearance for the different groups of mice. For instance, for each treatment-season combination, the ages and weights at puberty were compared for both disappearing and non-disappearing mice.

Similarly, the ages and weights at disappearance were compared for both pubertal and non-pubertal mice.

Age at Disappearance vs Age at Puberty

In all three seasons (regardless of treatment), mice which disappeared from the population did so very soon after (< eight days) reaching puberty (Table 3.15; see also Figures 3.8-10). The latency

Table 3.15 Latency to disappear following attainment of puberty.

	Summer 1981	Spring 1982	Summer 1982
Treatment	N X days ± (S.E.)	N X days ± (S.E.)	N X days ± (S.E.)
Melatonin	11 1.9 (1.4)	32 2.7 (0.8)	14 6.5 (2.0)
Control	13 3.7 (1.5)	37 4.0 (1.5)	14 7.7 (2.6)
Difference Between Treatments (t)	1.71	0.86	0.70
Probability	0.10 > p > 0.05	p > 0.30	p > 0.40

to disappear following puberty was not significantly different for melatonin-treated individuals vs controls. Latency to disappear was greater, however, in the Summer 1982 season compared to the other two seasons.

The overall simple linear regression equations for age at disappearance vs age at puberty were significant for melatonin-treated mice in the Summer 1981 ($r^2 = 0.81$; $F = 36.71$; $df = 1/9$; $p << 0.001$, Figure 3.8), Spring 1982 ($r^2 = 0.69$, $F = 67.20$; $df = 1/30$; $p << 0.001$, Figure 3.9), and Summer 1982 ($r^2 = 0.74$; $F = 35.12$; $df = 1/12$; $p << 0.001$, Figure 3.10). Similarly, for control-treated mice, the regression equations for age at disappearance vs age at puberty was significant for all three seasons (Summer 1981: $r^2 = 0.45$; $F = 8.82$,

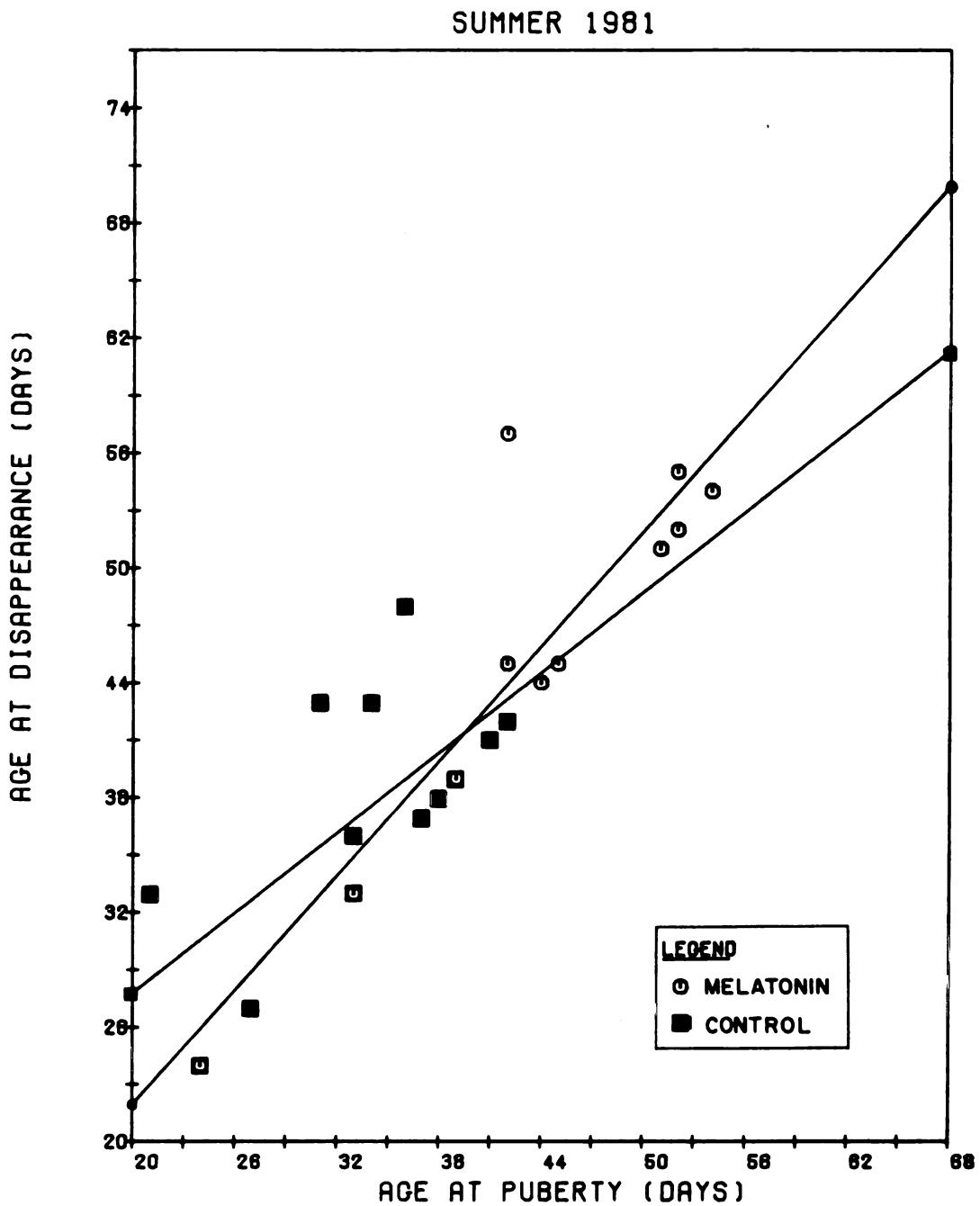


Figure 3.8 Relationship between age at disappearance and age at puberty for mice in the Summer 1981. The following regression equations are for melatonin-treated and control-treated mice respectively: $Y = 0.99X + 1.94$ ($n = 11$, $r^2 = 0.81$); $Y = 0.70X + 13.81$ ($n = 13$, $r^2 = 0.45$).

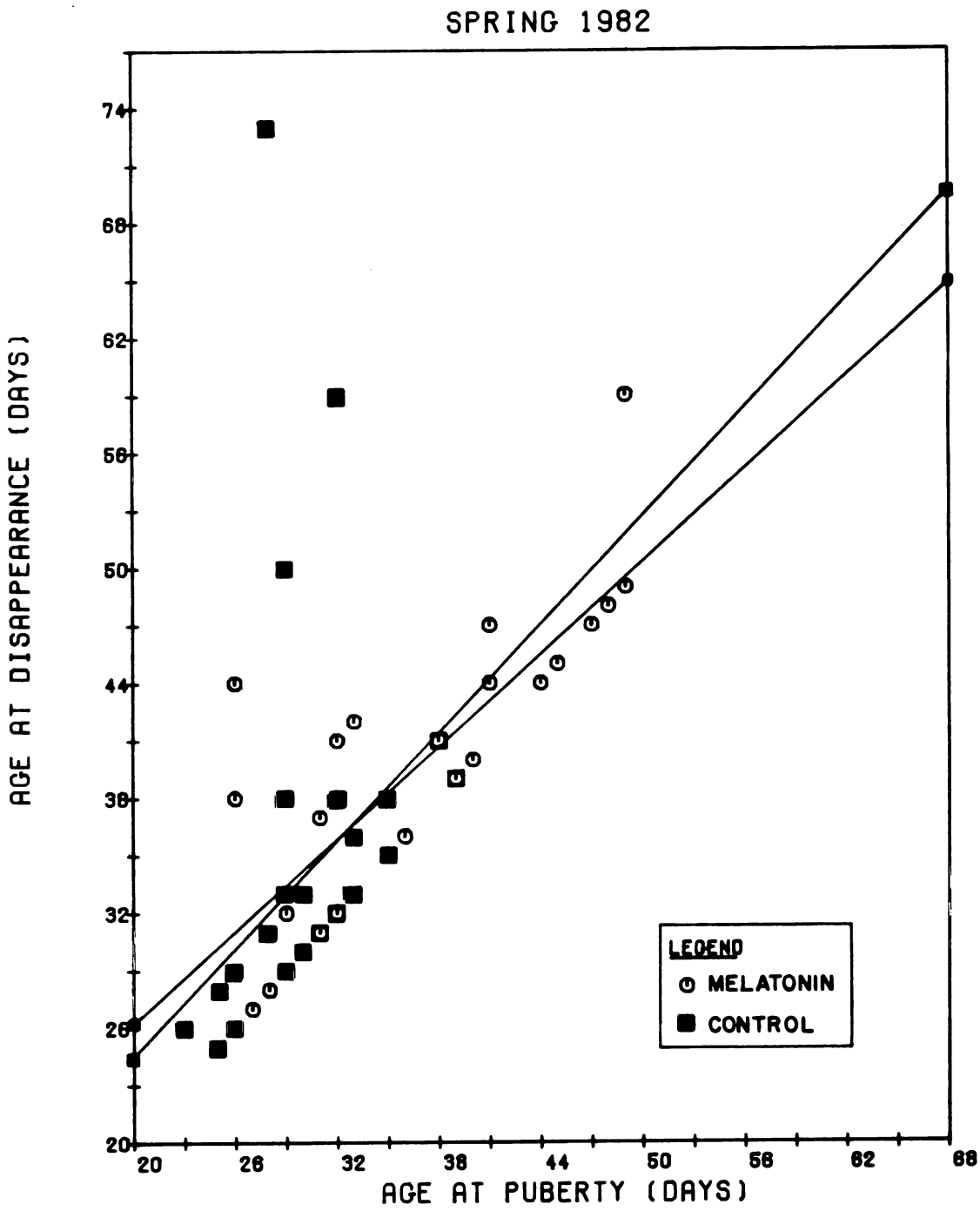


Figure 3.9 Relationship between age at disappearance and age at puberty for mice in the Spring 1982. The following regression equations are for melatonin-treated and control-treated mice, respectively: $Y = 0.80X + 10.16$ ($n = 32$, $r^2 = 0.69$); $Y = 0.94X + 5.72$ ($n = 37$, $r^2 = 0.13$).

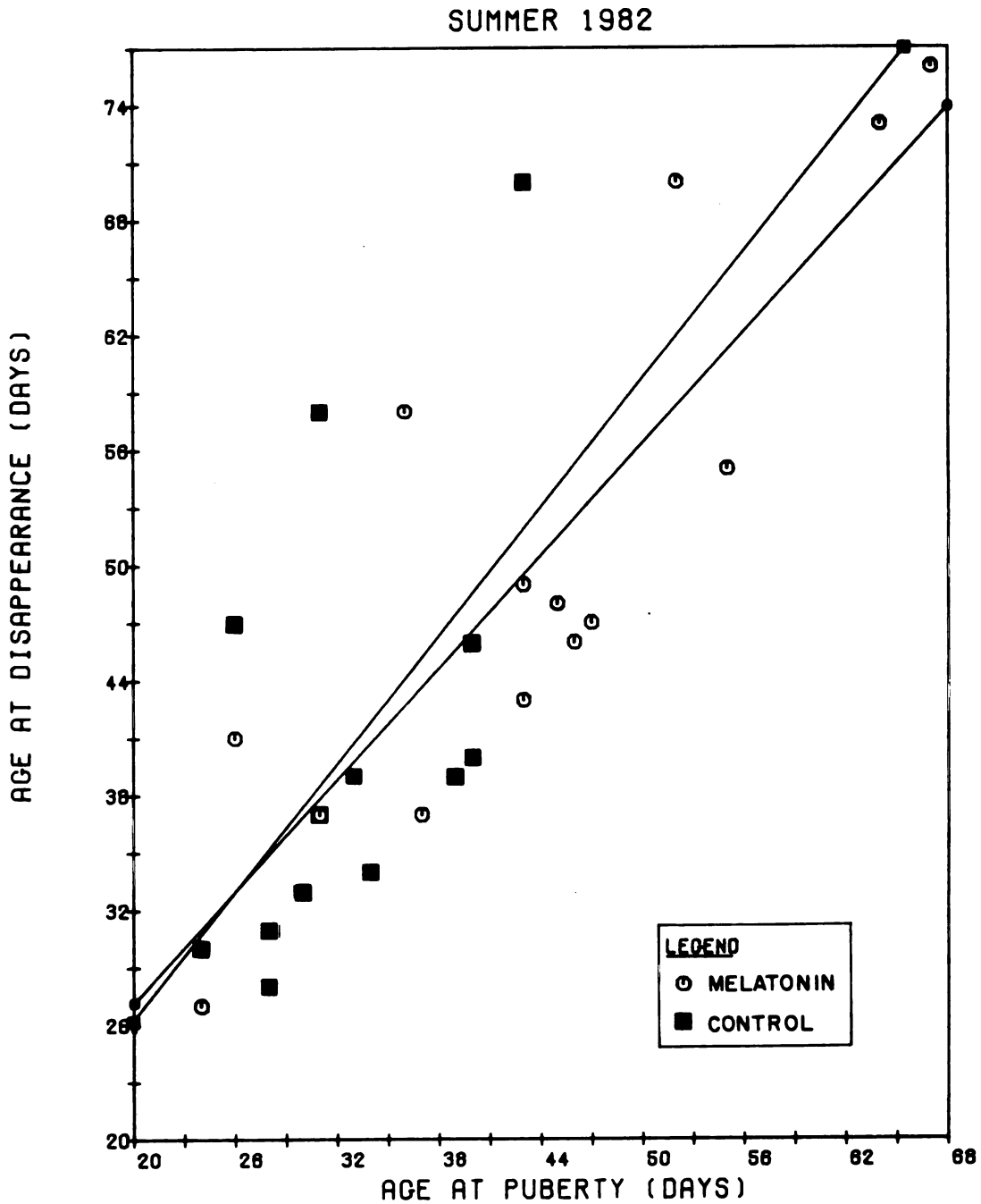


Figure 3.10 Relationship between age at disappearance and age at puberty for mice in the Summer 1982. The following regression equations are for melatonin-treated and control-treated mice, respectively: $Y = 0.97X + 7.65$ ($n = 14$, $r^2 = 0.74$); $Y = 1.12X + 3.96$ ($n = 14$, $r^2 = 0.30$).

df = 1/11, p = 0.013, Figure 3.8; Spring 1982: r^2 = 0.30; F = 5.32; df = 1/12; p = 0.040, Figure 3.10).

I compared the regression equations of melatonin-treated mice and controls in each season and found no significant differences in their slopes (Summer 1981: t = 0.74; df = 20; p > 0.40; Spring 1982: t' = 0.27; df ≃ 63; p > 0.50; and Summer 1982: t = 0.23; df = 24; p > 0.50). The assumption of equal variances about the regression equations necessary for this analysis was not violated.

When I compared the age at disappearance for mice that did or did not become pubertal, significant differences were found only for control-treated mice in the Summer 1981 and Spring 1982 seasons. In both of these seasons, mice used in the regression analyses (i.e. those which became pubertal prior to disappearing) disappeared at a later age than those mice which were not included in the regression (Summer: t' = 2.90; df ≃ 18; p = 0.009; Spring 1982: t = 4.55; df 49; p < 0.001). The comparison of ages at puberty for mice that did or did not subsequently disappear revealed a significant difference only for melatonin-treated mice in the Summer 1981. In this season, mice used in the regression analysis (i.e. those which attained puberty and subsequently disappeared) reached puberty at a later age than those mice which were not included in the regression (t' = 3.24; df≃12; p < 0.05).

Weight at Disappearance vs Weight at Puberty

The overall simple linear regression equations for weight at disappearance vs weight at puberty were significant for melatonin-treated mice in the Summer 1981 (r^2 = 0.70; F = 22.17; df = 1/9; p < 0.005, Figure 3.11) and Spring 1982 (r^2 = 0.55; F = 35.81; df = 1/29;

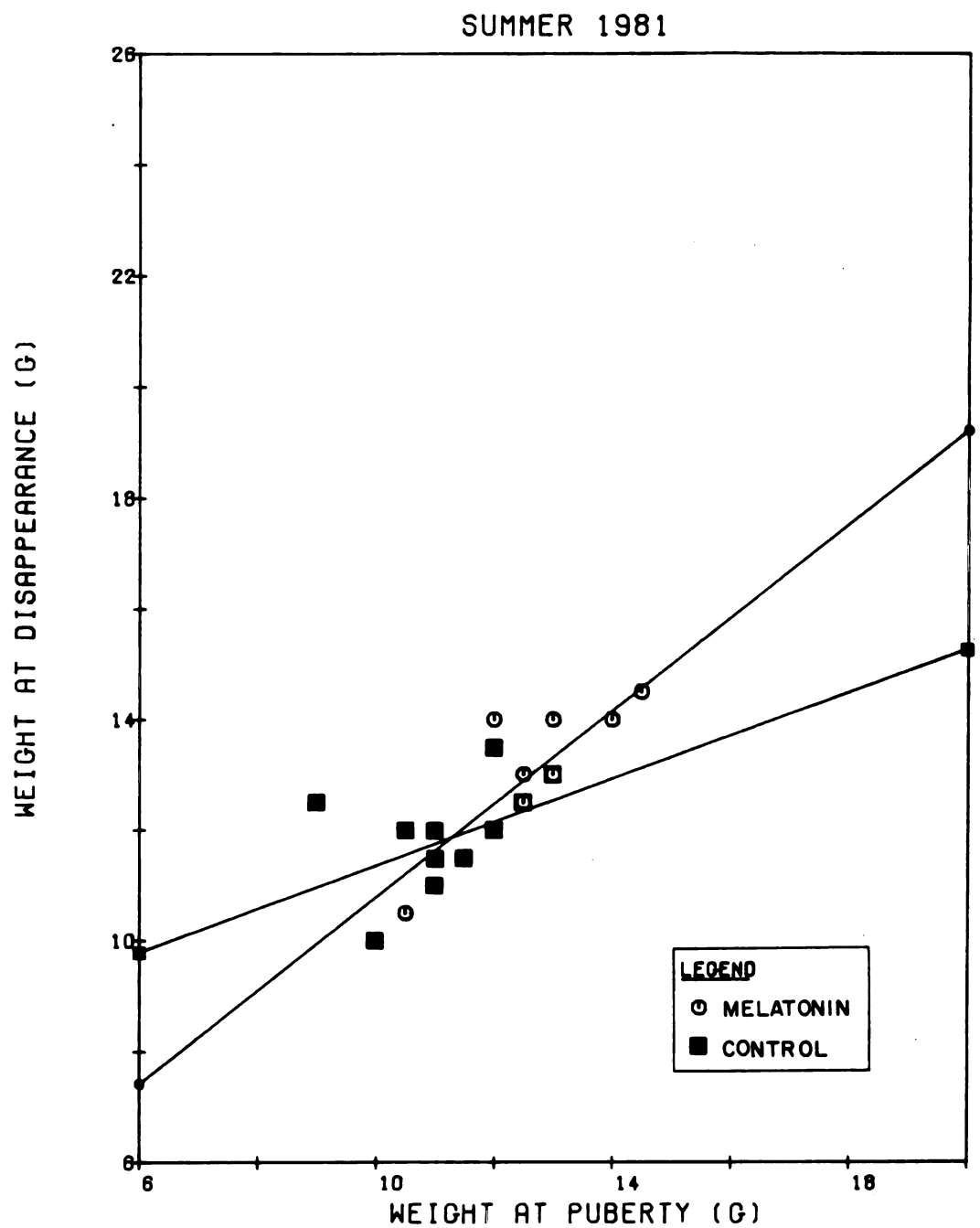


Figure 3.11 Relationship between weight at disappearance and weight at puberty for mice in the Summer 1981. The following regression equations are for melatonin-treated and control-treated mice, respectively: $Y = 0.84X + 2.36$ ($n = 11$, $r^2 = 0.70$; $Y = 0.39X + 7.47$ ($n = 13$, $r^2 = 0.21$).

$p << 0.001$, Figure 3.12), but not Summer 1982 ($r^2 = 0.42$; $F = 3.58$; $df = 1/12$; $p = 0.083$, Figure 3.13). For control-treated mice, the regression equation for weight at disappearance vs weight at puberty was significant in the Spring 1982 ($r^2 = 0.35$; $F = 8.87$; $df = 1/34$; $p << 0.012$, Figure 3.12), but not Summer 1981 ($r^2 = 0.21$; $F = 2.92$; $df = 1/11$; $p = 0.115$; Figure 3.13).

I compared the regression equations of melatonin-treated mice and controls in each season and found no differences in their slopes for Summer 1981 ($t = 1.10$; $df = 20$; $p > 0.40$), Spring 1982 ($t = 1.00$; $df = 63$; $p > 0.40$), or Summer 1982 ($t = 0.55$; $df = 24$: $p > 0.50$).

When the weight at disappearance for mice that did or did not become pubertal was compared, significant differences were found only for melatonin- and control-tested mice in the Spring 1982. In this season, mice used in the regression analysis (i.e. those which became pubertal prior to disappearing) weighed more at disappearance than those mice which were not included in the regression (Controls: $t' = 3.33$; $df \simeq 45$; $p < 0.005$; Melatonin-treated mice: $t = 2.34$; $df = 39$; $p = 0.024$). I found no significant differences when I compared the weight at puberty for mice that did or did not subsequently disappear.

EXPERIMENT 3.2: FALL DISPERSAL IN JUVENILES: EFFECTS OF STIMULATING SEXUAL BEHAVIOR

The general hypothesis tested in this experiment is that dispersal is more likely to occur in juvenile *P. m. bairdi* that are sexually active than non-sexually active.

Materials and Methods

On the day of tagging, juveniles were temporarily removed from their nest-boxes and brought into the laboratory to receive an implant

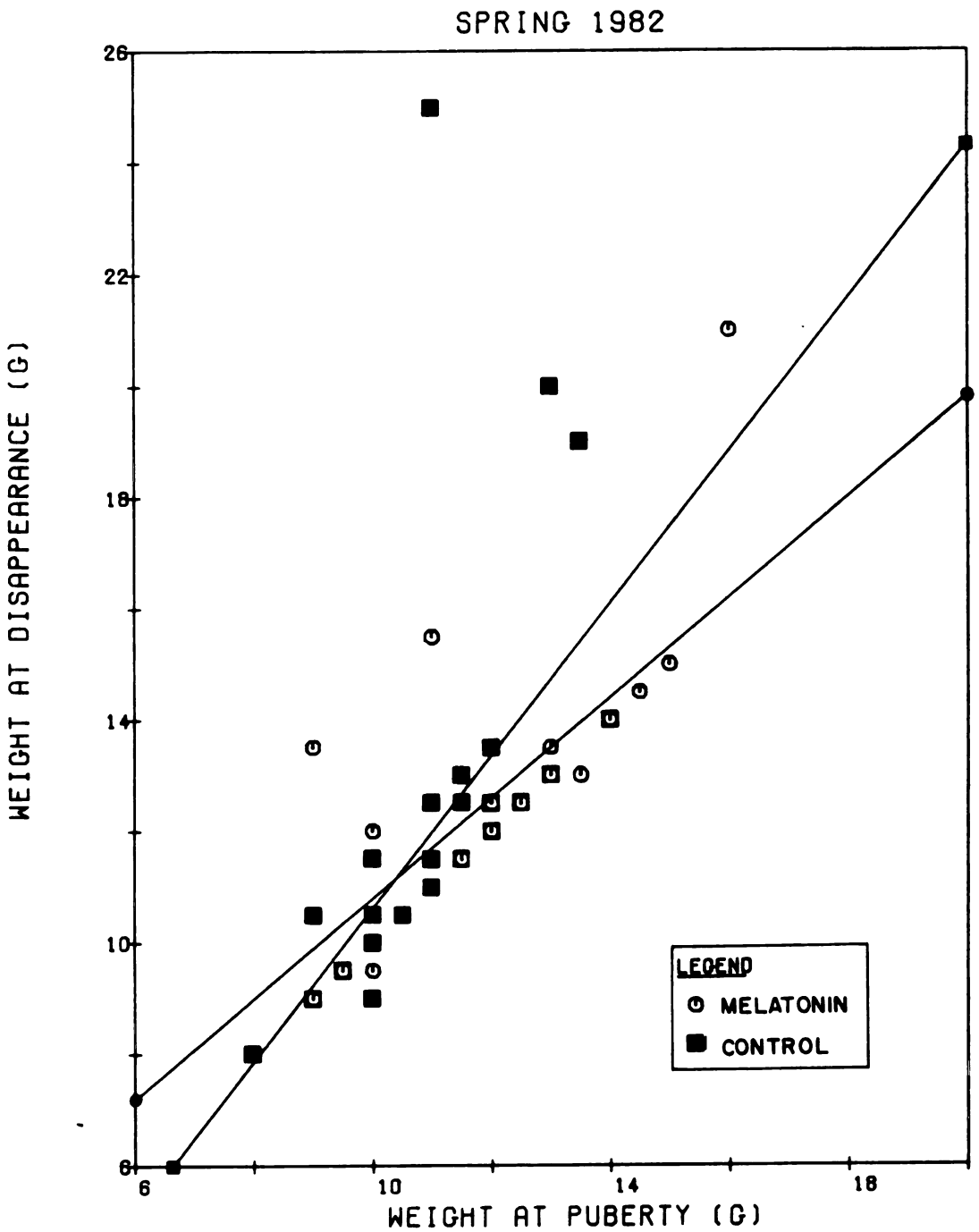


Figure 3.12 Relationship between weight at disappearance and weight at puberty for mice in the Spring 1982. The following regression equations are for melatonin-treated and control-treated mice, respectively: $Y = 0.90X + 1.77$ ($n = 31$, $r^2 = 0.55$); $Y = 1.37X - 3.11$ ($n = 36$, $r^2 = 0.35$).

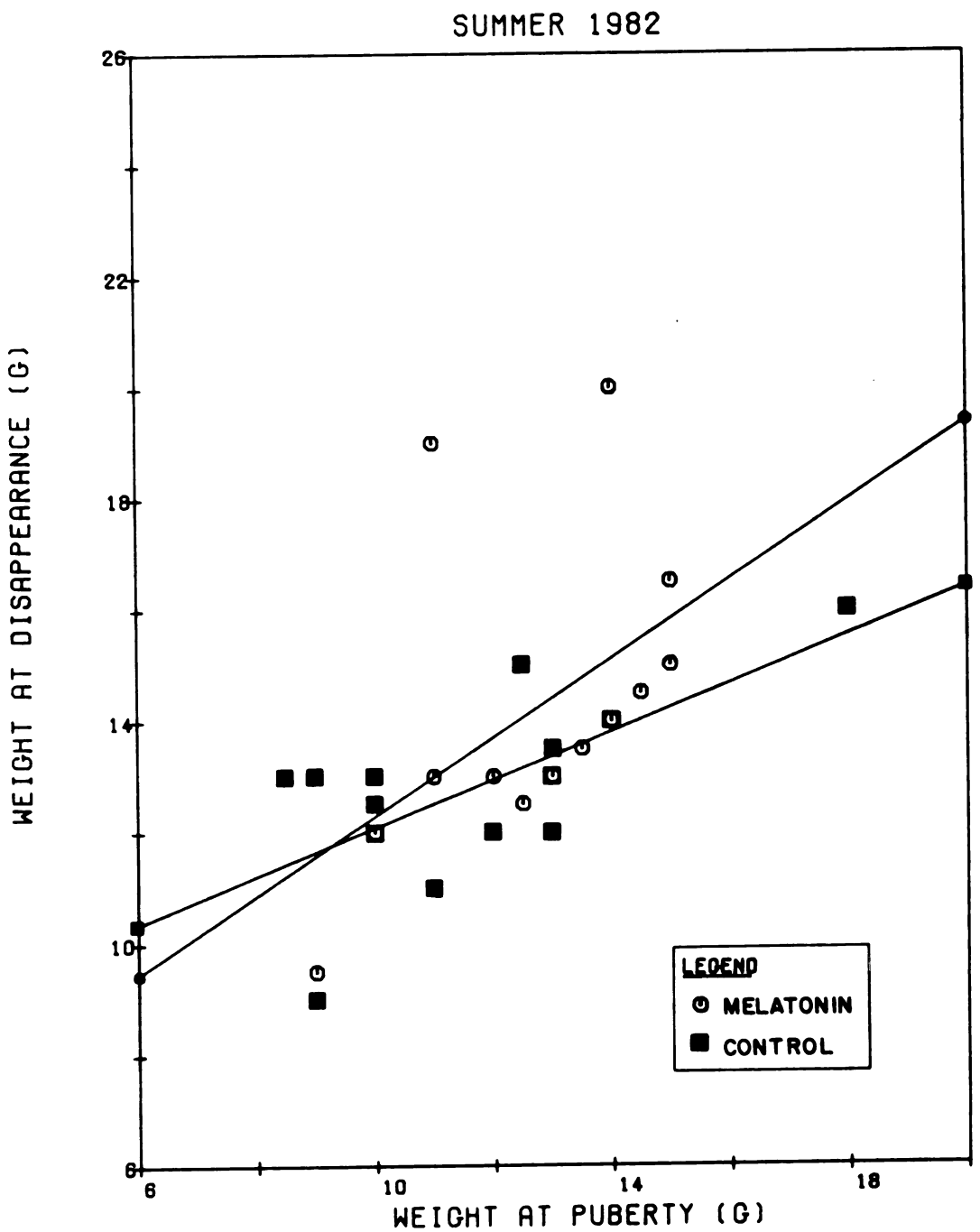


Figure 3.13 Relationship between weight at disappearance and weight at puberty for mice in the Summer 1982. The following regression equations are for melatonin-treated and control-treated mice, respectively: $Y = 0.71X + 5.21$ ($n = 14$, $r^2 = 0.23$); $Y = 0.43X + 7.78$ ($n = 14$; $r^2 = 0.42$).

treatment. Juvenile males from each litter randomly received either a testosterone propionate (TP) or control implant. Females from each litter received either an estradiol benzoate (EB) or control implant. Following the procedures of Clemens and Pomerantz (1982), males were subcutaneously implanted with either an empty (control) 10 mm length of Silastic capsule (Dow Corning Corp., 1.47 mm i.d. x 1.95 mm o.d.) or one containing finely ground TP. Similarly, females received either an empty capsule or one filled with finely ground EB. These implant dosages are known to induce copulatory behavior among male P. m. bairdi and receptivity among female P. m. bairdi (L. Clemens, S. Pomerantz; pers. comm.).

Following implantation (within four hours), mice were returned to their appropriate nest-boxes. On all subsequent nest-box checks, implant-treated mice were checked by palpation to confirm the presence of the implant. One individual lost its implant and was therefore discarded from any of the analyses.

Analysis

The following three hypotheses concern the effect of gonadal steroid treatment on puberty. Although it was predicted that steroid treatments would stimulate sexual activity, gonadal development should not be affected.

1. The probability of ultimate attainment of puberty by juveniles in the population is independent of treatment (TP, EB, or control).
2. Age at puberty is independent of treatment.
3. Weight at puberty is independent of treatment.

The remaining hypotheses pertain to the general prediction that dispersal will be more likely to occur, and at an earlier age, among steroid-treated individuals than controls. Dispersal here is defined as it is in Experiment 3.1.

1. Steroid-treated individuals are more likely to disappear from the population than control-treated individuals.
2. Steroid-treated individuals will disappear from the population at an earlier age than control-treated individuals.
3. Steroid-treated individuals will weigh less at disappearance than will control-treated individuals.
4. Resident, steroid-treated individuals are more likely to make inter-couplet movements than resident, control-treated individuals.
5. Steroid-treated mice are more likely to be captured in peripheral or perimeter traplines than control-treated mice.

I also predicted that disappearing mice are more likely to be pubertal than non-pubertal. Furthermore, I predicted that a positive relationship exists between age at puberty and age at disappearance. I also anticipated that the weight of individuals at puberty will be positively associated with weight of individuals at disappearance.

Various parametric and non-parametric tests were used to analyze the data: Chi-square tests of idependence (X^2), t-tests (t, t'), analysis of variance (one-way), simple linear regression (r^2), and Mann-Whitney U test of independence. T-tests, one-way ANOVAS, and linear regression were conducted with the aid of SPSS programs (T-TEST, ONE-WAY, REGRESSION, and PLOT). Mann-Whitney U tests were

used when the more strict assumptions of the parametric tests were violated.

Results

On October 30, November 3, and 4, I recorded five weasel attacks on families in the mouse cities. In these five predations by two known M. nivalis, at least ten adults and 20 juveniles were known to have been killed. In most of the attacks the adult females were nursing young; thus, four litters were either killed altogether or reduced in size. To eliminate the possibility of including lost individuals into the category of disappeared instead of killed, I chose to eliminate from the analyses all juveniles that survived the attempted predation. Two weasels were caught; one was in the act of killing nestlings when it was discovered and removed; the other was trapped in a live-trap adjacent to one of the arenas. The four affected families were replaced (except for any survivors) with five new breeding pairs from the laboratory mouse colony (see General Materials and Methods above).

Effects of Treatments on Attainment of Puberty

The null hypothesis that ultimate attainment of puberty is independent of hormone treatment was rejected for males (TP vs Control: $x^2 = 12.08$, df = 1, $p < 0.002$, Table 3.16), but accepted for females (EB vs Control: $x^2 = 0.90$, df = 1, $p > 0.60$, Table 3.16). Significantly more TP-treated males (in the population at least 21 days) became pubertal than control-treated males. In fact, none of the control males attained puberty during the course of the

Table 3.16 Frequencies with which males and females (for each treatment) became pubertal or remained non-pubertal.

	Sex			
	Male		Female	
Response	TP	Control	EB	Control
Pubertal	10	0	7	4
Non-Pubertal	1	5	1	2
Totals	N=11	N=5	N=8	N=6
	$X^2 = 12.08$, df = 1, $p < 0.002$		$X^2 = 0.90$, df = 1, $p > 0.60$	

experiment. Females in the EB treatment group were no more likely to become pubertal than females in the control group.

Due to the small sample sizes and unequal variances, I used Mann-Whitney U tests to compare the age at puberty of controls and steroid-treated mice. Since no control males attained puberty, no comparisons with TP-treated males was possible (see Figure 3.14). For females, where a comparison of controls and EB-treated females was possible, I found no significant different in the age at puberty ($U = 7$, $p = 0.115$; Figure 3.14), although EB-treated females were slightly younger compared to controls.

Although the age at puberty for EB-treated females was not significantly less than the age at puberty for controls, their weights were significantly different ($U = 4$, $p = 0.036$, Figure 3.15). EB-treated females weighed less at puberty than controls. Again, no

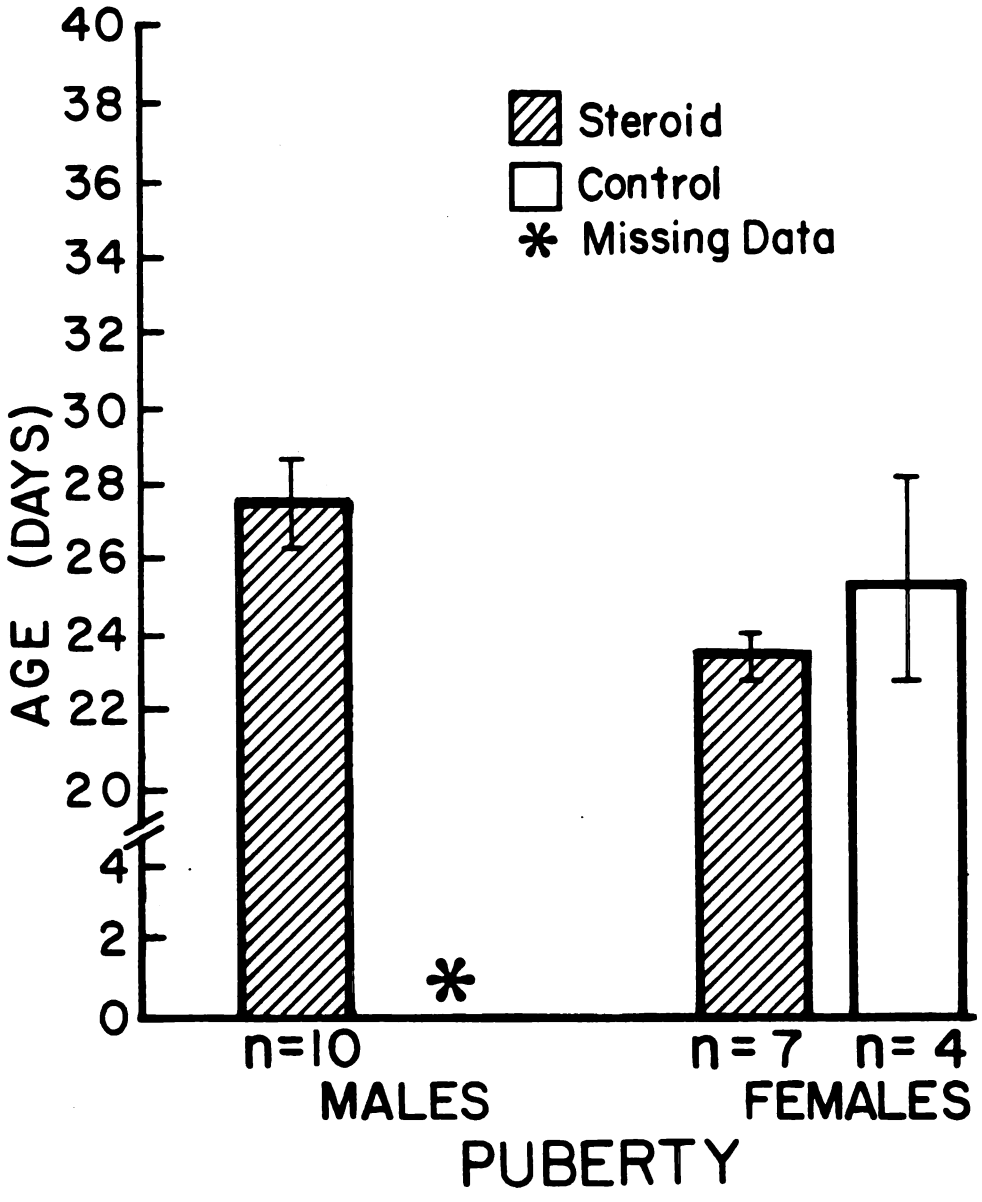


Figure 3.14 Mean age at puberty. Vertical lines indicate ± 1 S.E.

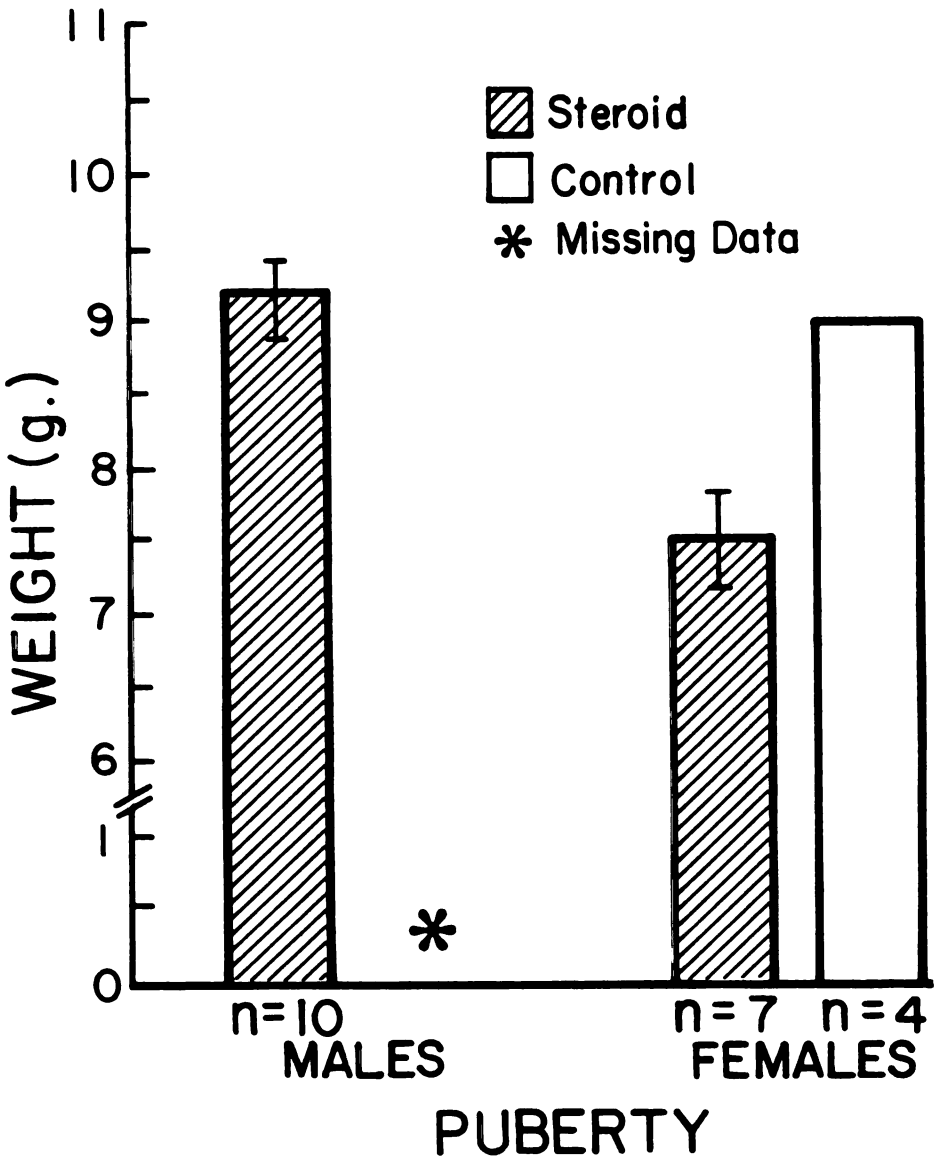


Figure 3.15 Mean weight at puberty. Vertical lines indicate $\pm$ 1 S.E.

comparisons of weight at puberty for TP-treated males vs controls was possible (see Figure 3.15).

No females from either treatment group became pregnant during the duration of the experiment.

Effects of Treatment on Dispersal

Following the procedures described above in Experiment 3.1 for distinguishing stayers from mice which disappear, I tested the hypothesis that steroid-treated mice were more likely to disappear than controls. For males and females, occupancy (stay vs disappear) was found to be independent of hormone treatment (Males: one-tailed $X^2 = 0.90$, df = 1, $p > 0.30$; Females: one-tailed $X^2 = 0.57$, df = 1, $p > 0.30$; Table 3.17).

Table 3.17 Frequences with which males and females (for each treatment) disappeared from the population or stayed. Stayers are individuals which remained in the population until at least the median age of occupancy for all treated mice (33 days).

	Sex			
	Male		Female	
Response	TP	Control	EB	Control
Stay*	4	5	5	3
Disappear	6	3	3	4
Totals	N=10	N=8	N=8	N=7
	**$X^2 = 0.90$, df = 1, $p > 0.30$		**$X^2 = 0.57$, df = 1, $p > 0.30$	

*Individuals that remained in population until at least the median age of occupancy for all treated mice (33 days)

**One-tailed.

An unexpected result was the finding that control males disappeared from the population at an earlier age than did TP-treated males ($U = 1$, $p = 0.024$, Figure 3.16). Control females, on the other hand, did not differ from EB-treated females with regard to the age of the their disappearance ($U = 5$, $p = 0.429$; Figure 3.16). Furthermore, the weights at disappearance did not differ for steroid-treated mice vs controls for either males or females (Males: $U = 8$, $p = 0.452$; Females: $U = 5$, $p = 0.429$, Figure 3.17).

As an alternative measure of dispersal-related movement, I assessed the rate of inter-couplet movement for mice that did not disappear (in this case, mice which resided in the population for at least 33 days, the median length of occupancy). Due to the small sample of responses for mice from either the TP or EB treatment groups, all steroid-treated mice were pooled for the analysis. Inter-couplet movement was independent of treatment (one-tailed $X^2 = 0.02$, $df = 1$, $p > 0.30$, Tab.e 3.18). Very few resident mice from either treatment group made inter-couplet movements. The live-trapping data from this experiment revealed a pattern similar to that found in Experiment 3.1; that is, few juveniles were ever found in traps on either the peripheral or perimeter traplines. Two mice were captured on the peripheral trapline and one was caught on the perimeter trapline. Two (one male, one female) of the three captured mice were pubertal at the time of capture.

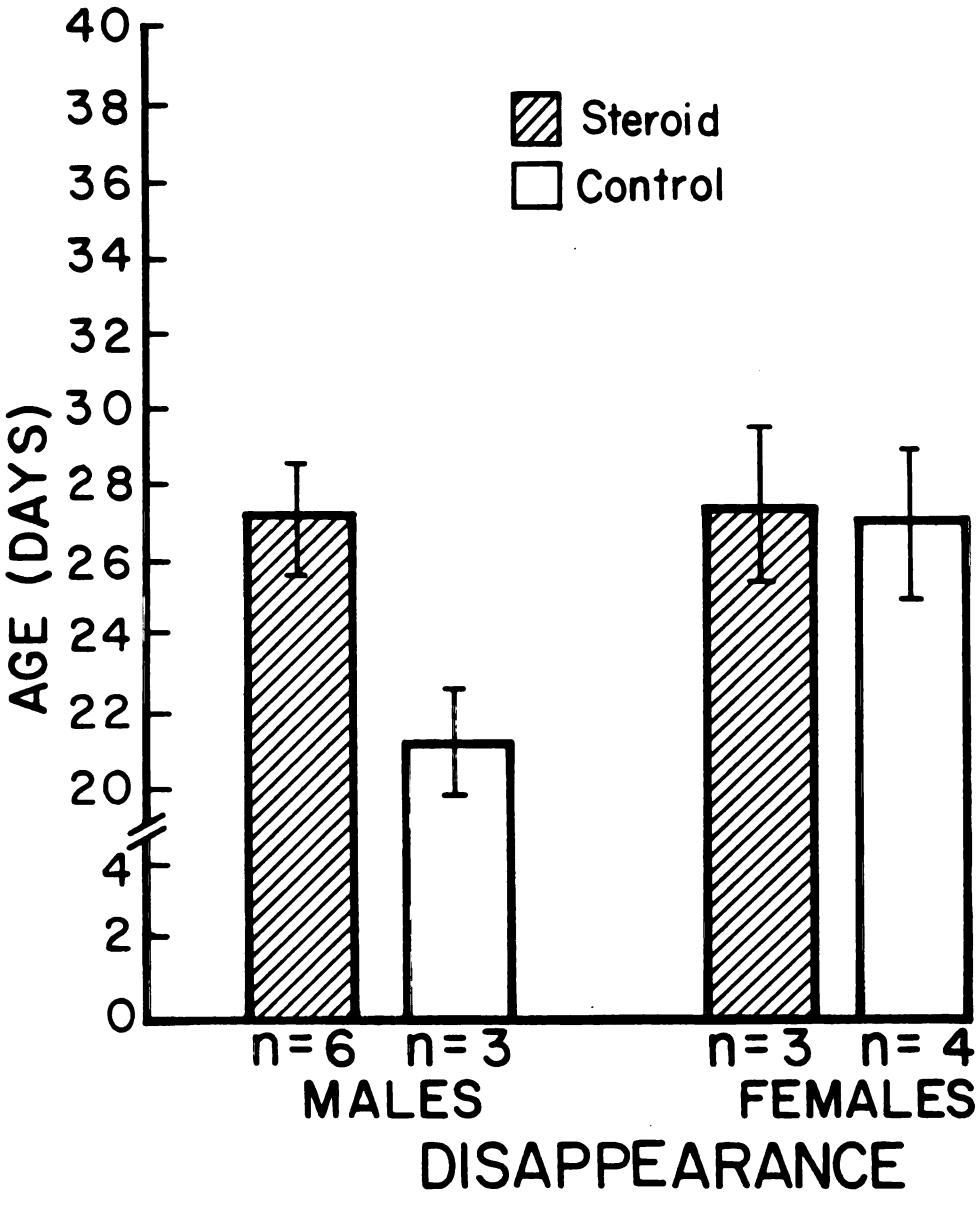


Figure 3.16 Mean age at disappearance. Vertical lines indicate $\pm$ 1 S.E.

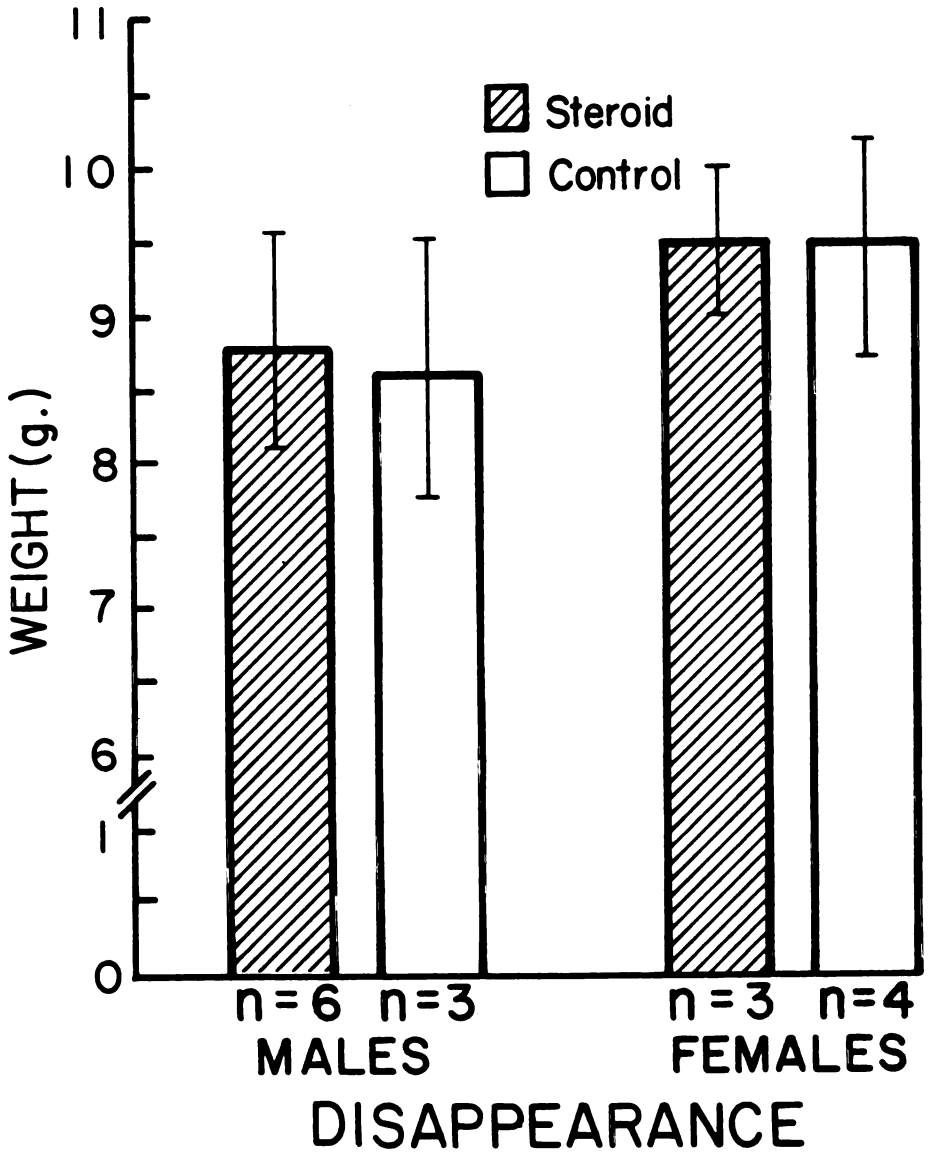


Figure 3.17 Mean weight at disappearance. Vertical lines indicate ± 1 S.E.

Table 3.18 Frequencies with which steroid- (EB and TP pooled for males and females) and control-treated stayers made at least one inter-couplet movement.

	Treatment (Sexes Pooled)	
Response	Steroid (EB, TP)	Control
Move	2	2
No Move	7	6
Totals	N=9	N=8

**X^2 = 0.02, df = 1, p > 0.30

*Individuals that remained in population until at least the median age of occupancy for all mice (33 days).
**One-tailed.

Relationships Between Attainment of Puberty and Dispersal

Mice which disappeared from the population were equally likely to be pubertal as non-pubertal (one-tailed X^2 = 1.0, df = 1, p > 0.10; Table 3.19). Further examination of these data revealed, however, that TP-treated males were more likely to be pubertal at disappearance than control males (X^2 = 5.65; df = 1, p < 0.05; Table 3.20). Steroid-treated females, on the other hand, did not differ from control females (X^2 = 0.06, df = 1, p > 0.60, Table 3.20). Repression analyses of age and weight at disappearance on age and weight at puberty were attempted on TP-treated males, EB-treated females and controls (sexes combined). The rationale behind utilizing only those animals which became pubertal prior to their disappearance is explained above in Experiment 3.1. The regression of weight at disappearance on weight at puberty was not possible for control males

Table 3.19 Frequency with which individuals were pubertal at disappearance.

Responses	Observed	Expected
Pubertal	10	8
Non-Pubertal	6	8
Totals	N=16	N=16

$X^2 = 1.00$, df = 1, $p > 0.10$

Table 3.20 Frequencies with which males and females (for each treatment) were pubertal at disappearance.

	Sex			
	Male		Female	
Response	TP	Control	EB	Control
Pubertal	5	0	2	3
Non-Pubertal	1	3	1	1
Totals	N=6	N=3	N=3	N=4
	$X^2 = 5.65$, df = 1, $p < 0.05$		$X^2 = 0.06$, df = 1, $p > 0.60$	

because all of these animals weighed the same at puberty (the independent variable).

Age at Disappearance vs Age at Puberty

Regardless of treatment (steroid or control), mice which disappeared from the population did so very soon (x = 3 days; Table

3.21, see also Figures 3.18-19) after showing signs of puberty. The latency to disappear from the population following the attainment of puberty was not significantly different for steroid-treted mice vs controls.

Table 3.21 Latency to disappear following attainment of puberty among mice that became pubertal before disappearing.

Treatment	N	$\bar{x}$ days $\pm$ (S.E.)
TP	5	1.2 (1.20)
EB	3	4.0 (0.87)
Control	3	5.0 (2.00)

The simple linear regression equations for age at disappearance vs age at puberty were not significant for the steroid-treated mice (TP-males; $r^2 = 0.56$; $F = 3.76$; $df = 1/1$; $p = 0.148$; EB-females: $r^2 = 0.84$; $F = 5.33$; $df = 1/1$; $p = 0.260$). The slope of the regression line for each steroid treatment group was not significantly different from the slope of the control group regression line.

Weight at Disappearance vs Weight at Puberty

The overall simple linear regression equation for weight at disappearance vs weight at puberty was significant for TP-treated males ($r^2 = 0.88$; $F = 21.21$; $df = 1/3$; $p = 0.019$), but not for EB-treated females ($r^2 = 0.89$, $F = 8.33$; $df = 1/1$; $p = 0.212$). As explained above, a regression analysis was not possible for the control group.

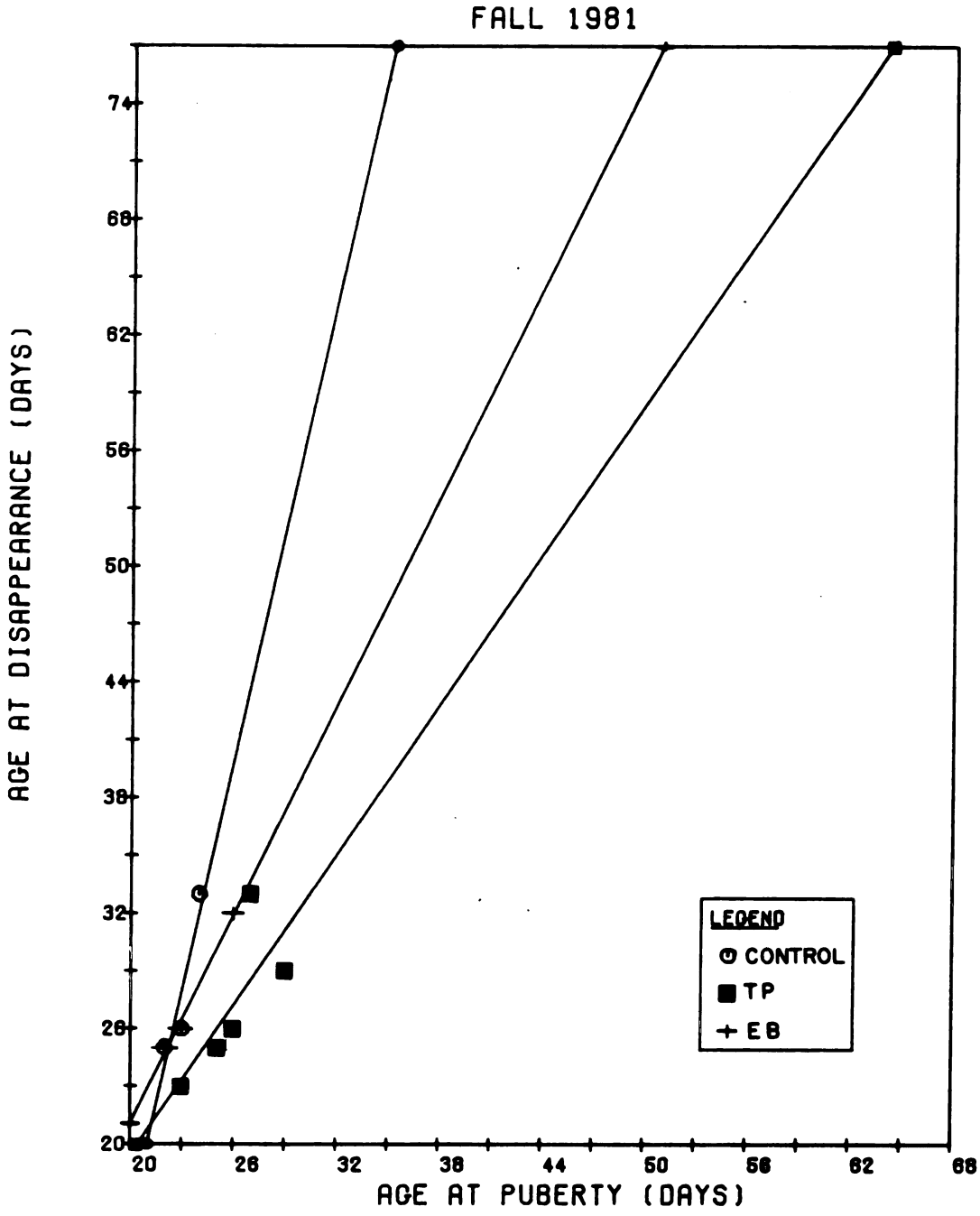


Figure 3.18 Relationship between age at disappearance and age at puberty for mice in the Fall 1981. The following regression equations are for control-treated, TP-treated, and EB-treated mice, respectively. $Y = 4.00X - 64.00$ ($n = 3$, $r^2 = 0.84$); $Y = 1.30X - 6.60$ ($n = 5$, $r^2 = 0.56$); $Y = 1.81X - 15.11$ ($n = 3$, $r^2 = 0.98$).

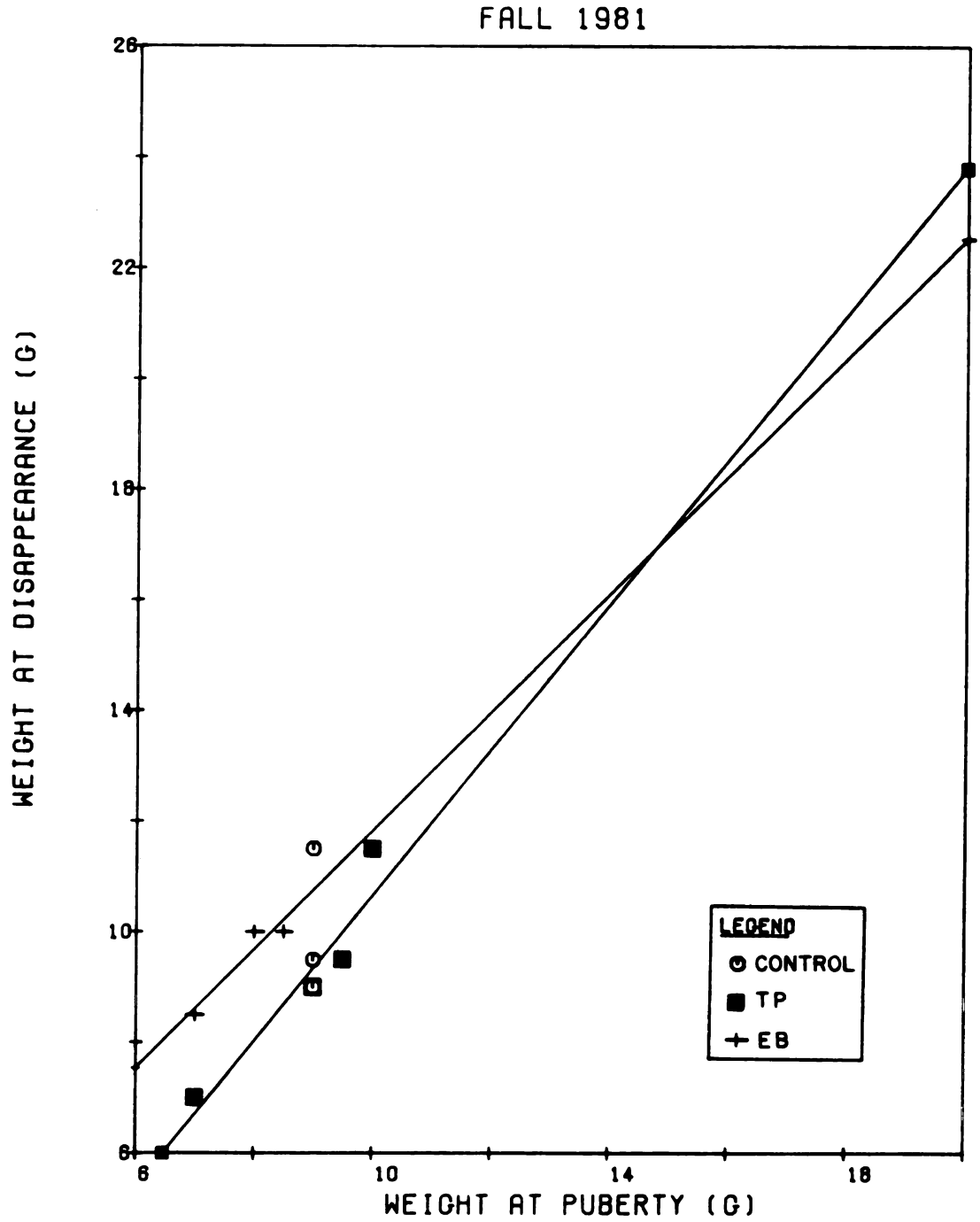


Figure 3.19 Relationship between weight at disappearance and weight at puberty for mice in the Fall 1981. The following regression equations are for TP-treated and EB-treated mice, respectively. A regression analysis was not possible for control-treated mice (see text): $Y = 1.32X - 2.52$ ($n = 5$, $r^2 = 0.82$); $Y = 1.07X + 1.11$ ($n = 3$, $r^2 = 0.89$).

Discussion

This study aimed to investigate the role of sexual maturation in the postnatal dispersal of juvenile *P. m. bairdi*. Although many authors have noted that dispersers are commonly young, pubertal individuals, few have argued that the postnatal dispersal of juveniles may be causally related to their sexual maturation. Instead, many have implied that dispersal is a density dependent phenomenon and that individuals, particularly the very young or very old, are forced to disperse from an area in response to limitations in such critical resources as food and living space (Christian, 1970; Krebs, 1978a; Lidicker, 1975). King (1983) questioned the importance of density in controlling dispersal and found, instead, by controlling several density related variables, that dispersal in juveniles was associated primarily with seasonal patterns in their sexual recruitment to the population. He proposed that juveniles of either sex disperse from their natal site in search of mates. Furthermore, it was proposed that this sexual search behavior by juveniles commences with the onset of their sexual maturity, a time when pubertal mice are attracted to relevant sexual stimuli in their environment.

In partially controlled experiments with semi-natural populations of *P. m. bairdi*, I tested predictions of the sexual search hypothesis by manipulating the expression of sexual maturity in juveniles. Juvenile dispersal (i.e. disappearance) is characteristically high in the spring and summer, seasons in which juveniles are known to be sexually recruited into the breeding population (King, 1983). In the first experiment I attempted to delay the dispersal of spring and summer-born juveniles by delaying their sexual maturation through

exogenous treatment with the antigonadal hormone, melatonin. In the fall of the year, however, juveniles typically fail to breed and are less likely to disperse. Thus, in the second experiment I attempted to stimulate dispersal in juveniles via their treatment with the gonadal steroids, testosterone propionate and estradiol benzoate.

Critical to both of the experiments described here was the assumption that gonadal steroids can facilitate the expression of mate-searching behavior. For instance, in the first experiment, melatonin was expected to indirectly delay sexual searching in mice by retarding their gonadal maturation and subsequent production of gonadal steroids. In the second experiment I expected that direct exogenous treatment of juveniles with gonadal steroids would stimulate sexual search behavior. Turning to the literature on hormones and behavior for support, one finds that the expression of sexual behavior in P. m. bairdi and other species is clearly dependent on the presence of gonadal steroid hormones (Pomerantz et al., 1983; see also reviews by Larsson, 1979; Morali and Beyer, 1979). As evidence for this relationship, one finds that in prepubertal mice and in adult mice that have been castrated, exogenous treatment with gonadal steroids can either initiate or restore normal sexual behavior (Larsson, 1979). In most studies though, gonadal steroids are known to exert control of the copulatory elements of normal sexual behavior, i.e. lordosis in females, and mounting, intromission, and ejaculation in males. Little is known, however, about how other, pre-copulatory behaviors (e.g. mate-seeking behavior) are affected by these hormones. One recent study, however, has shown that gonadal steroids can activate courtship behavior as well as copulatory behavior in male P. m. bairdi

(Pomerantz, et al., 1983). Gonadal steroids can also stimulate locomotory and exploratory behaviors, which are surely associated with mate-seeking activity (Blizard, 1983; Holekamp, 1982; Mather, 1981, Moore, 1965). For example, implants of testosterone in males, and estradiol in females, are known to increase certain components of locomotor activity in hamsters (Ellis and Turek, 1979; Morin, et al., 1977). Holekamp (1982) suggested that gonadal steroids can stimulate natal dispersal in ground squirrels through their mediating effects on juveniles' exploratory behavior.

If sexually motivated mice are, indeed, predisposed to exhibit increased locomotory and exploratory behaviors as a result of the influence of gonadal steroids, one should expect these mice to move from a home nest at puberty in search of a mate. Evidence from an earlier field study supports this contention. Howard (1949) found it unlikely that juvenile P. m. bairdi breed within close vicinity of their natal nest. He demonstrated that more than half of the young mice he studied moved away from their natal home range before breeding. If, as King (1983) and I have proposed, pubertal juveniles disperse in search of potential mates, one should see sexual search behavior manifested in measurable movements away from their area of birth.

In the present study, I selected inter-couplet movement as one of three possible indicators of sexual search behavior. During both experiments, at least half of the couplets at the mouse cities were occupied by other mice at any given census. It stands to reason that if sexually mature mice were dispersing in search of mates, the search may very well extend to other couplets. In the first experiment, mice

which were treated with melatonin to delay sexual maturation should, according to the sexual search hypothesis, be less likely to make inter-couplet movements than controls. The results indicated that, of all the mice that resided in the nest-boxes for at least 42 days (median age of residency), melatonin-treated mice were, indeed, unlikely to move from their natal couplet (Table 3.13a). Although there was no direct dependence of these movements on sex or season, closer analysis revealed that, when controlled for season, control males were more likely to move from their natal couplet than melatonin-treated males. The contingency test (Table 3.13d) suggests that melatonin treatment is probably not affecting the males' tendency to move differently than it affects females because, in both sexes, melatonin-treated individuals were at least two times more likely to remain in their natal couplet than move. Control mice of either sex, on the other hand, were more likely to move from the natal couplet than not move. When sex was controlled, a significant treatment effect was found only in the summer 1982 season. Again, the factor most likely to be responsible for this significant effect was the tendency of control mice to be more inclined to move from their natal couplet.

In the second experiment, steroid-treated mice were just as likely to move from their natal couplet as controls (Table 3.18). The proportion of all mice that moved was lower in the fall experiment than in the spring and summer. In spite of the small sample sizes, this apparent low rate of movement by mice born in the fall seemed to be fairly typical of fall-born mice from previous years (King, 1983).

Evidence of behavior related to sexual searching need not be restricted to inter-couplet movements. Mate seeking behavior is likely to involve an exploration of the individual's surroundings in general. Any widespread exploration of the environment by an individual is certain to increase its chances of encountering a potential mate (Mather, 1981). Unfortunately, nest-box censuses only revealed where mice rested during the day, and these checks were made only every third day. Nocturnal movements could be made by mice that appeared, from the census of nest-boxes, to be ensconced in one arena or couplet. I hoped, therefore, that by monitoring traplines that surrounded the mouse cities I would be able to identify mice that were moving away during the night from their natal couplet and into the surrounding fields. If the sexual search hypothesis is correct, one should expect to find that sexually mature mice, or mice that were treated with gonadal steroids, would be more likely to explore the surrounding fields and become trapped than sexually immature mice. Unfortunately, too few juveniles were trapped in any season to allow a reliable interpretation of the data. Of those mice that were trapped, neither sex, hormone treatment, nor reproductive condition were distinguishing characteristics. It was surprising, in light of the relatively large juvenile component to the population in most seasons, that so few juveniles were caught in the traps. Nevertheless, this low capture rate corresponds well with the trapping results of an earlier study at the mouse cities (King, 1983).

The results of the present study and that of King (1983) show that most mice either remained in the mouse cities and occupied nest-boxes, or disappeared from the population, although some mice

only occupied nests periodically. For purposes of this discussion, disappearance is defined as a permanent, discontinued daytime occupation by a mouse of any nest-box.

In the first experiment, half of all tagged juveniles disappeared from the population in each season by the time they reached 42 days of age. Of those mice which disappeared by this age 71% (82/115) were controls (Table. 3.8a). In all three seasons, controls were more likely to disappear than melatonin-treated mice. In the fall experiment, steroid-treated mice of either sex were just as likely to disappear as controls of either sex (Table 3.17). In the fall, nearly one out of every two mice disappeared prior to reaching 33 days of age. It is interesting to compare these rates of disappearance with those from earlier studied populations at the mouse cities. In his study of one summer and two spring seasons, King (1983) reported that 75.4% (129/171) of all tagged juveniles (from first and second litters only) disappeared from the population by the end of each ten week experiment. This value is remarkably similar to that obtained for control mice in the first experiment of the present study, where 73.9% (82/111) disappeared prior to reaching 42 days of age (Table 3.8a). Thus the high rate of loss for controls in the present study appears to be fairly typical of other spring and summer populations. Compared with this high rate of juvenile disappearance, the loss among melatonin-treated mice was significantly lower (Table 3.8a: 31.4% - 33/115). This value for the melatonin-treatment group is more typical of mice in the fall, a season when juveniles are more likely to be sedentary. In two previous fall experiments, King (1983) reported that, on the average, 33.9% (40/118) of the juveniles were lost from

the population. Compared with this value, mice in the present fall experiment were more likely to disappear, but this rate of disappearance was still below the loss rate recorded for control mice in the spring and summer seasons.

The value for disappearance described above for melatonin-treated mice is somewhat misleading, however, because it is only a measure of those mice which disappeared prior to reaching 42 days of age. Many more melatonin-treated individuals actually disappeared, but did so after 42 days of age. Mice that were treated with this hormone disappeared, on the average, 9 days later than controls (Figure 3.6). In fact, this difference in age at disappearance can be seen even in comparisons with untreated mice from 4 previous spring and summer seasons at the mouse cities (from King, 1983; Table 3.22). The ages

Table 3.22 Age at disappearance for melatonin-treated mice and untreated mice from 6 previous seasons.

Season	Age at Disappearance (Days) $\bar{x}$	(± S.E.)
Summer 1979	30.11	$(0.84)^{a}$
Spring 1979	30.44	$(1.68)^{ab}$
Spring 1980	33.41	$(1.64)^{abc}$
Summer 1980	36.10	$(1.04)^{bd}$
Spring 1982*	38.84	$(1.35)^{cde}$
Fall 1979	39.27	$(2.80)^{abef}$
Fall 1978	39.59	$(3.09)^{abef}$
Summer 1981*	44.80	$(1.87)^{df}$
Summer 1982*	47.79	$(2.83)^{f}$

*Experimental seasons (all others are baseline seasons; see text for explanation). Means sharing a common letter are not significantly different.

at disappearance for melatonin-treated mice were consistently higher in all seasons except for 2 previous fall seasons. Table 3.23 indicates that the ages at disappearance for controls and untreated mice from the previous seasons were not significantly different. In addition to a treatment effect on disappearance, there was also a seasonal effect. The proportion of disappearing mice was highest in the spring season (Table 3.8b), and spring mice disappeared at an earlier age than summer mice (Figure 3.4).

Table 3.23. Age at disappearance for control mice and untreated mice from 6 previous seasons.

Season	Age at Disappearance (Days) $\bar{x}$	(± S.E.)
Summer 1979	30.11	(0.84)[a]
Spring 1979	30.44	(1.68)[ab]
Spring 1982*	31.10	(1.26)[ab]
Spring 1980	33.41	(1.64)[ab]
Summer 1981*	33.85	(1.87)[ab]
Summer 1980	36.10	(1.04)[b]
Summer 1982*	36.96	(2.83)[ab]
Fall 1979	39.27	(2.80)[ab]
Fall 1978	39.59	(3.09)[ab]

*Experimental seasons (all others are baseline seasons; see text for explanation). Means sharing a common letter are not significantly different.

At this point in the discussion I would like to address the question of why control mice in the first experiment were more likely to disappear, and disappear earlier, than melatonin-treated mice. This question might be easier to answer if I knew whether these two groups of mice disappeared for the same reason. Unfortunately, it is impossible to know for certain why any mouse would disappear. We can

be certain, however, that mice which disappeared from a nest-box either left the nest-box permanently, or died there.

The results of this experiment suggest that nest mortality does not explain the observed differences in the rates and ages of disappearance. There is little indication to suggest that control individuals were more likely to die at the nest, or die earlier there, than melatonin-treated mice. With the exception of the deaths of some young nestlings due to abandonment by their mother, few mice were found dead in the nest-boxes. In the three seasons of this experiment only 4 dead juveniles were recovered from the nests. The cause of death was determined for only one of these mice, a control juvenile that was killed and partially eaten in the spring 1982 by a weasel, presumably M. nivalis. Incidentally, in the same season, one entire litter of preweanling mice was found dead in a nest-box. Of each mouse killed by a weasel there was evidence of the characteristic puncture wound at the base of the skull. In order for nest predation to explain the earlier disappearance of control mice, predators would be expected to prey selectively on control mice that were younger than melatonin-treated individuals. Although it is possible that more mice could have been preyed upon at the nest, particularly by weasels, it is unlikely that a predator would behave in the manner alluded to above. For instance, in weasel attacks, the weasel typically kills most or all of the occupants of a nest-box or even an arena (Murphy, pers. obs.). Because occupied arenas were typically inhabited by relatively equal proportions of controls and melatonin-treated mice (usually littermates), weasel predation would not explain why control

mice occupants disappeared at an earlier age than their melatonin-treated counterparts.

Other predators, too, were unlikely to be the cause of the differential disappearance among treatment groups. Although the arenas and concrete nest-boxes were accessible to the agile, small-bodied weasels, they probably afforded the mice considerable protection from other potential predators, particularly snakes, shrews, raccoons, and owls. Snakes were sometimes common in nest-boxes that lie outside of the arenas (0 nest, Figure 3.2). The arena wall was effective in preventing most snakes from gaining entry to the arenas although they were sometimes found in nest-boxes inside of the arena. Another potential predator that was rarely seen inside of an arena was the short-tailed shrew. Shrews and snakes were both probably excluded from the arenas due to the elevated entrance hole on the arena wall. Raccoons, on the other hand, were sometimes persistent in gaining entry to the arenas by climbing over the arena wall. This problem was severest in the summer 1982 during which several raccoons developed a theretofore rarely observed ability to open the lids of several nest-boxes. During the course of approximately one week in this season, raccoons entered several arenas formerly occupied by tagged mice and removed the lids to all of the nest-boxes inside. I suspected that in a few of these arenas, the raccoons may have caught and killed the occupants. The removal of the troublesome raccoons through intensive live-trapping, and the development of a nest-box security lid, prevented any further nest disturbances by raccoons in that season. The arguments presented above suggest that predation at the nest can not adequately explain

the observed patterns of disappearance in the present study. Therefore, in all likelihood, mice that disappeared probably moved permanently away from the nest-boxes. If this is true, why, then, did control mice leave their nest at an earlier age than melatonin-treated individuals?

It is interesting to note here that melatonin treatment alone could affect the activity of treated mice. In experiments with rats, melatonin treatment can depress wheel-running activity (Wong and Whiteside, 1968). Chronic administration of melatonin was also effective in suppressing locomotor activity in house sparrows (Hendel and Turek, 1978). When the melatonin implant was removed from a bird, locomotor activity was restored to pre-treatment levels. Whether melatonin in the present study delayed the departure of treated mice from their nest because of its antigonadal effects or due to the suppression of locomotor activity (or both), is unknown.

Although I have argued that the movement of mice from their natal area results from their initiation of mate-searching behavior, the possibility remains that these movements represent a motivated search for some other resource that is not available in the vicinity of the natal nest. Some potentially limited resources that could influence these movements include food, water, refugia and/or nesting sites. If, for the sake of argument, control mice were assumed less tolerant of a resource limitation than melatonin-treated individuals, and more likely to move in search of it, then a shortage of a critical resource at the natal nest could explain their earlier disappearance. For example, perhaps controls and melatonin-treated mice differed in their nutritional requirements. The results show that controls were,

indeed, lighter in weight than melatonin-treated mice when they disappeared. In spite of ample food supplies at the nests, one could argue that controls were forced to leave the nest to locate some deficient element to their diet. This argument can be disputed, however, on two grounds. Firstly, although controls weighed less at disappearance (Figure 3.7), the observed weight difference was more likely to be due to the chronological differences in age at disappearance between controls and melatonin-treated mice than to a deficiency in growth in the former. Secondly, there is laboratory evidence which indicates that melatonin-treatment does not significantly affect body weight in P. leucopus (Johnston and Zucker, 1980a; Lynch et al., 1978; see also Results, Chapter 2). Thus, it is unlikely that nutrition contributed much to the observed treatment differences in disappearance. The same can probably be said of water. During dry periods I was careful to provide extra water at each arena.

Although controls were more likely to move from their natal couplet or disappear than melatonin-treated mice, they probably did not do so for a lack of available nests or refugia. There were always surplus nest-boxes available throughout the duration of each experiment. For instance, over half of the available arenas ($x = 18.03$), and nearly one-third of the available couplets ($x = 5.31$), were unoccupied at any given census. Nearly 4 arenas ($x = 3.67$) were never occupied at all during each ten week experiment. King (1983) reported similar values for unoccupied arenas ($x = 19.2$; $x = 5.0$).

It is also unlikely that parasitism or disease could explain any treatment effect on disappearance. One could argue, though, that controls may be more inclined to leave the nest-boxes than

melatonin-treated mice because the former were more susceptible to parasitism or disease at the nest. For instance, many common mouse parasites (e.g. fleas and mites) are sometimes more common in a nest than on a mouse (Whitaker, 1968). Perhaps, then, controls leave the nest to avoid infestation. This is unlikely, however, because almost all mice in the present study, regardless of treatment, already had some parasites (fleas) before they disappeared. Of the few observed incidences of parasitism by botfly larvae (Cuterebra sp.), just as many control mice were afflicted as melatonin-treated individuals (5 cases each).

To summarize the arguments presented so far, it appears that nestbox-related mortality or parasitism cannot adequately explain why melatonin-treated mice disappeared from their natal couplet at an older age than controls. It also seems improbable that melatonin-treated individuals and controls would respond differently to potential deficiencies in food or nesting sites. Furthermore, because predation, food supply, and nesting sites were at least partially controlled in each season, it is doubtful that these factors could explain the seasonal effects on disappearance. Why, then, did spring mice disappear at an earlier age than summer mice, and why did melatonin-treated mice disappear at an earlier age than controls?

An important clue to an understanding of the observed treatment and seasonal effects may be found in the association between disappearance and the attainment of puberty. Irrespective of treatment, the majority of mice which disappeared did so very soon (2-8 days) after reaching puberty (Table 3.15). Indeed, regression analyses of the mice that disappeared following puberty revealed that

the age at puberty is a good predictor of age at disappearance. This relationship held for controls as well as melatonin-treated mice, regardless of season (Figures 3.8-10). This relationship serves to explain why melatonin-treated individuals disappeared at a later age than controls.

Disappearance and puberty were also dependent on season. For example, the proportions of mice that reached puberty and disappeared were both highest in the spring (Tables 3.2c, 3.8b). Furthermore, spring mice reached puberty at an earlier age than summer mice (Figure 3.4).

One possible explanation for the observed difference in the age at puberty and in the proportion of pubertal mice could be the concomitant seasonal change in the photoperiod. Photoperiods changed substantially from one season to the nest. Daylength increased from about 13.5 to 15.3 (1.8) hours in the spring experiment and decreased from 15.1 to 12.6 (2.5) hours in the summer and from 12.2 to 9.5 (2.7) hours in the fall. Although the total length of daylight available to the mice in the summer and spring seasons was comparable, the direction of change in the daylength differed. Perhaps it is this decline in daylength, independent of treatment effect, which is responsible for summer mice reaching puberty in fewer numbers and at an older age than spring mice. Seasonal changes in photoperiod are known to exert a strong influence on the reproductive development in P. maniculatus and other temperate-climate small mammals (e.g. Johnston and Zucker, 1980b,c; Petterborg and Reiter, 1980; Whitsett et al., 1983).

Another notable difference between the spring and summer seasons is the lower density of mice found in the two summers. Compared to the large spring season population, there were 38% fewer treated juveniles (at least 30 days old) present in the summer 1982 population and 89% fewer in the summer 1981 population (Table 3.2c). These differences can be attributed primarily to the variation in the size of litters born to the introduced adult females. It is not intuitively clear if the difference in densities could explain the observed pattern of pubertal development and disappearance in the different seasons. Because the spring season was not replicated, the possibility remains that the seasonal difference is due to a sampling error. Nevertheless, it appears that the seasonal effect on puberty probably accounts for the observation that spring mice disappeared at an earlier age and in greater proportions than summer-born mice.

This close association between age at disappearance and ontogenetic maturation of the gonads lends credence to the argument that gonadal hormones may be important in activating mate-seeking activity in mice. If gonadal steroids are important in this regard, then mice that are treated with these hormones should be more inclined to depart their natal area, and leave at an earlier age, than mice which received no treatment. The results of the second experiment revealed, however, that steroid-treated mice were just as likely to disappear as controls (Table 3.17). The expected treatment effect on age at disappearance was also not realized. In fact, control males disappeared at a younger age than steroid-treated males (Figure 3.16). In spite of the small sample sizes, I will offer several possible explanations for these results. Firstly, the gonadal steroids chosen

for the exogenous treatments simply may not have stimulated mate-seeking behaviors, though they may be involved in activating other sexual behaviors. Perhaps other gonadal hormones, or even different metabolites of the ones used in the present study (TP, EB) may be more important in facilitating the search component of sexual behavior. Indeed, other investigators have shown that the degree to which sexual behavior in P. m. bairdi is affected by gonadal steroids is influenced by the particular sexual behavior under consideration (Pomerantz, et al., 1983).

Another reason why gonadal steroids were possibly ineffective could be that they were administered to mice at an age at which behavioral development was relatively insensitive to the hormones. In a recent unpublished study, Holekamp (1982) tested the hypothesis that concurrent, circulating gonadal steroids cause natal dispersal in juvenile Belding's ground squirrel (Spermophilus beldingi). Her data contradicted this prediction and indicated, instead, that perinatal exposure to androgens (in males) is required to activate dispersal later on.

Although perinatal exposure to gonadal steroids may be important for the dispersal of juveniles in the present study, I would argue that circulating gonadal hormones associated with puberty are also critical for the expression of mate-seeking dispersal. I believe this is true because in mice treated with melatonin, puberty and dispersal were both delayed.

Finally, I wish to consider the possibility that by treating mice in the fall with gonadal steroids I was actually able to stimulate natal dispersal in not only the steroid-treated mice but also in the

controls. I consider this as a possibility because of the following observation. The results of this study indicated that the ages at disappearance for controls as well as steroid-treated mice were significantly younger than that of untreated mice from 2 previous fall seasons (King, 1983). In fact, mice in the present fall experiment disappeared, on the average, at an earlier age than mice from any previously studied season at the mouse cities (Tables 3.24-26). I offer the following explanation for why controls and treated mice both disappeared at such an early age. Following their treatment with gonadal steroids, mice may increase their exploratory activity and soon move from their natal couplet. At this time in the year, the breeding season is nearing its end and fewer individuals, particularly juveniles, will be in breeding condition. Thus, sexually stimulated juveniles may be expected to leave their natal area in search of the remaining individuals in breeding condition (see Nadeau et al., 1981). Control individuals, in turn, may then disperse due to their perception of other active individuals in the population.

Unfortunately, any of the above scenarios could serve to explain the disappointing results of the steroid experiment. Clearly, more research is required to determine the roles that sexual maturation and gonadal hormones have in mediating postnatal dispersal. Although I have demonstrated in the first experiment that a delay in sexual maturation in juveniles can result in a delay in their natal dispersal, I can only assume that gonadal hormones may be involved. These field experiments should be repeated, but an attempt should be made to determine if a causal relationship exists between particular gonadal steroids and dispersal. One way of accomplishing this would

Table 3.24 Age at disappearance for testosterone-treated mice and untreated mice from 6 previous seasons.

Season	Age at Disappearance (Days) $\bar{x}$	(± S.E.)
Fall 1981*	26.75	(1.26)[b]
Summer 1979	30.11	(0.84)[bc]
Spring 1979	30.44	(1.68)[abc]
Spring 1980	33.41	(1.64)[abc]
Summer 1980	36.10	(1.04)[a]
Fall 1979	39.27	(2.80)[ac]
Fall 1978	39.59	(3.09)[ac]

*Experimental season (all others are baseline seasons: see text for explanation). Meaning sharing a common letter are not significantly different.

Table 3.25 Age at disappearance for estradiol-treated mice and untreated mice from 6 previous seasons.

Season	Age at Disappearance (Days) $\bar{x}$	(± S.E.)
Fall 1981*	27.40	(1.54)[b]
Summer 1979	30.11	(0.84)[bc]
Spring 1979	30.44	(1.68)[abc]
Spring 1980	33.41	(1.64)[abc]
Summer 1980	36.10	(1.04)[a]
Fall 1979	39.27	(2.80)[ac]
Fall 1978	39.59	(3.09)[abc]

*Experimental season (all others are baseline seasons; see text for explanation. Means sharing a common letter are not significantly different.

Table 3.26. Age at disappearance for control mice and untreated mice from 6 previous seasons.

Season	Age at Disappearance (Days) $\bar{x}$	(± S.E.)
Fall 1981*	27.40	(3.44)[b]
Summer 1979	30.11	(0.84)[bc]
Spring 1979	30.44	(1.68)[abc]
Spring 1980	33.41	(1.64)[abc]
Summer 1980	36.10	(1.04)[a]
Fall 1979	39.27	(2.80)[ac]
Fall 1978	39.59	(3.09)[ac]

*Experimental season (all others are baseline seasons; see text for explanation). Means sharing a common letter are not significantly different.

be to monitor blood steroid levels in the juveniles before they disperse. This approach is being attempted by I. McDonald and M. Taitt (in Taitt and Krebs, 1982) in a study designed to examine the role of gonadal steroids in controlling certain female behaviors in field populations of voles.

Although hormonal manipulation of animals in the field is becoming more common, the hormonal treatments are almost exclusively restricted to adult individuals (e.g. Krebs et al., 1977; Taitt and Krebs, 1982). Only in the present study and one by Holekamp (1982) were juveniles treated with hormones. Furthermore, most studies were designed to investigate aggressive behaviors. In these field studies on aggression, and in their laboratory counterparts (e.g. Whitsett et al., 1979), some degree of causal relationship was observed between gonadal hormones and aggression, particularly for adult males (see review by Bronson and Desjardins, 1971). Although the authors of

these studies did not examine juvenile dispersal in the field, many invariably suggested that, in the field, hormonally-mediated aggression in adults is important in controlling, among other things, mortality and dispersal of juveniles (Ayer and Whitsett, 1980), and recruitment of juveniles to the population (Whitsett et al., 1979). Some of these investigators, as well as others (Fairbairn, 1977a,b, 1978a; Healey, 1967; Sadlier, 1965), might argue, for example, that in the present study, pubertal juveniles were driven from their natal site by aggressive adult conspecifics. If sexual maturity in juveniles was an aggression-eliciting cue for adults, it is possible that juveniles were forced to disperse from their natal area only after attaining puberty. If this were true, adult aggression could explain the results of the present experiment where juveniles, irrespective of treatment, disappeared shortly after becoming pubertal.

This aggression-related argument, however, can be disputed on several grounds. Firstly, overt aggression among conspecifics has never been directly observed in natural populations (see Chapter 4). Even indirect evidence of aggression in the field is rare. In the present experiment only 5 juveniles in a total of 4 experimental seasons exhibited any signs of scars that may, or may not, have been the result of wounding. Secondly, the widely held notion that juvenile dispersers are forced out of their natal area by their parents needs to be re-examined in light of the discovery by Halpin (1981) that parents do not show aggression towards their young in P. m. austerus, and P. m. saturatus. Adult aggression is usually only documented under laboratory conditions in which adults are allowed to

interact with other adults, or with unrelated juveniles (e.g. Ayer and Whitsett, 1980; Rowley and Christian, 1976; Whitsett et al., 1979). In the present study, owing to the cohesive nature of the family groups (see also King, 1983), the adults most likely to be near the juveniles prior to their dispersal from their natal area are the parents. If, as suggested by Halpin, parents do not exhibit aggression towards their offspring, the juveniles must disperse on their own initiative. Furthermore, the fact that juveniles which remained in the population exhibited familial cohesion with their parents argues against aggression (see also King, 1983). Alternatively, aggression could be involved in provoking dispersal if adults other than the parents attack and drive out juveniles. This, too, is unlikely to have been important in the present study because adults from different family groups rarely intermingled (see also King, 1983). Halpin (1981:341) suggested that is possible that after a juvenile left its natal site, "the aggressive behavior of unrelated adults may have an effect on its survival and recruitment into the population." Even this type of aggression is probably rare in the present study because there was always an ample supply of space, food, and nesting sites available to support a growing population.

Although there is evidence from the daytime nest-box observations which indicates that juveniles are unlikely to be found with unrelated adults, I cannot be certain that this spacing pattern exists during the night, when mice are active and likely to be gone from the nest-boxes. For instance, could adults be overtly aggressive towards unrelated juveniles during nighttime encounters? If juvenile dispersal was the result of nighttime aggression by unrelated adults,

one should expect to find a high degree of interaction between unrelated adults and juveniles during the night. I tested this prediction in the next chapter by using radiotelemetric methods to study the patterns of nocturnal activity, space use, and nest-cohabitation among selected adult males.

CHAPTER FOUR

PATTERNS OF NOCTURNAL ACTIVITY, SPACE-USE AND NEST COHABITATION IN FREE-RANGING MALE *P. M. BAIRDI* AS REVEALED BY RADIOTELEMETRY

Introduction

Aggressive behavior of resident breeding adults towards juveniles has frequently been implicated as the primary cause for juvenile dispersal in *Peromyscus* spp. (e.g. Sadlier, 1965; Healey, 1967; Fairbairn, 1977a,b, 1978a). In fact, aggression has been invoked as an explanation for juvenile dispersal in many small mammals, including microtines (Chitty, 1955; Christian, 1971; Krebs, 1970; Myllymäki, 1977; Reich *et al.*, 1982). As far as I am aware, no one has yet directly observed aggression in unconfined mice in the field, although Terman (1961) described nocturnal observations of aggression in *P. m. bairdi* between residents and aliens tethered outside of the residents' nest-boxes. In addition, there is indirect evidence of aggression from wounding scars in microtines (Christian, 1971; Lidicker, 1973, 1980; Madison, 1980a; Rose and Gaines, 1976; Turner and Iverson, 1973), though Anderson (1980; see also Literature Review) questioned the validity of this measure. Most of the evidence for aggression between adults and juveniles comes primarily from observations of mice in arena encounters or enclosed populations. Results from these laboratory situations are often extrapolated to unconfined natural populations. Few investigators question the validity of these extrapolations; however, Anderson (1980) warned that "extrapolations from these

confined situations to nature can be justified only when supported by direct observations of undisturbed animals in the field." I took his recommendation and planned a direct, radiotelemetry study of activity patterns of free-ranging P. m. bairdi in an attempt to estimate the likelihood of adult-juvenile aggression in the field.

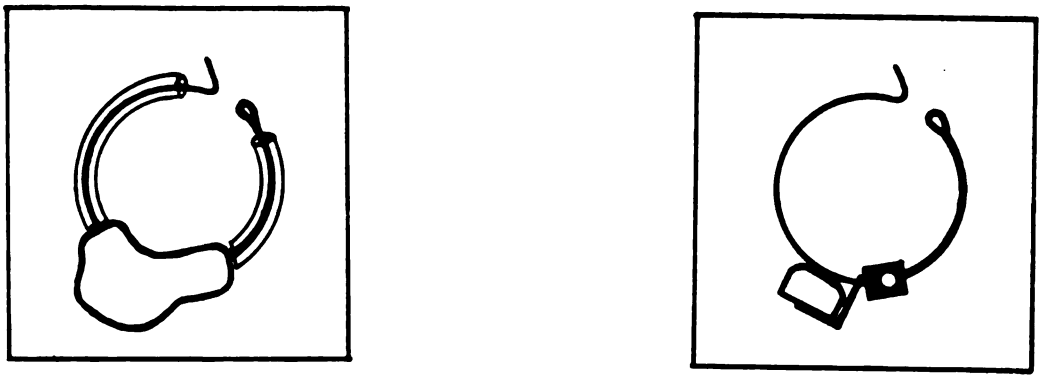
Healey (1967) examined the role of aggression in population regulation in deer mice and admitted that practically nothing is known about the way aggression occurs in the natural habitat. Healey hypothesized that aggressive male mice were more active and therefore more capable of occupying large home ranges than docile males. He tested the first part of the hypothesis and found that aggressive mice were more active than docile mice. He went on to suggest (1967:383) that "the number of social contacts a mouse makes must depend, in part, on how active it is. In this case, the aggressive mice would be more likely to encounter and threaten a strange juvenile." It was unfortunate that he could not test the second part of his hypothesis. In this experiment I used radiotelemetric methods to examine the likelihood of encounter between resident breeding adult males and other mice in a population with known familial composition.

Materials and Methods

The study site for the radiotelemetric analysis was the same as described for Experiments 3.1 and 3.2 (General Materials and Methods, Chapter 3). The animals used in this experiment consisted of 16 of the 17 mated adult male Peromyscus maniculatus bairdi introduced as members of the original bisexual pairs in the Fall 1981 and Spring 1982 seasons of Experiments 3.1 and 3.2 Nine mice were radiocollared in the Fall 1981 season and 7 mice were studied in the Spring 1982 season.

On the ninth day of confinement to the introduction couplet (see General Materials and Methods, Chapter 3), each adult male chosen for radiotracking was fitted with a miniature radiotransmitter which followed the design of Shields (1976). Each transmitter package consisted of transmitter elements, a battery, and an integral tuned-loop antenna that also served as the collar (Figure 4.1).

Figure 4.1 Schematic diagram of a radiocollar. The diagram on the right shows only the electronic components of the radiocollar. The one on the left shows a radiocollar that is potted with dental acrylic and fitted with a protective sleeve.



Prior to the attachment of a radiocollar to a mouse, the transmitter package was potted with dental acrylic to protect the electrical components from potential damage that could result from gnawing (Madison, 1977) or moisture. Finished radiotransmitter packages weighed from 1.9 to 2.4 g. No mouse was collared with a transmitter that weighed more than 15% of the animal's body weight. The radiocollar was fitted to the mouse by customizing the tuned-loop antenna to fit snugly around the neck. The collar and its circuitry were completed by soldering the ends of the antenna leads together with a low-wattage portable soldering gun. Observations of mice fitted with radiocollars of this design in a preliminary test of the transmitter's

efficacy indicated some skin irritation occurred from exposure to the bare wires of the antenna-collar. To solve this problem each collar was fitted with a small sleeve of plastic heat-shrink tubing. This sleeve prevented the wire antenna leads from causing undue irritation to the skin. Early attempts at attaching collars on non-experimental mice in the field resulted in less than satisfactory results. Therefore, all mice tested in this experiment were collared in the laboratory. Due to the incomplete synchrony in the introduction dates of the bisexual pairs (Table 3.1, Chapter 3) not all males in each season were collared on the same day, although each male was collared on the ninth day of its confinement to its couplet. Mice were removed from their respective couplets during the daytime and brought back to the laboratory for the attachment of a radiocollar. An attempt was made to return the collared mouse to its home couplet within four hours after being removed. All mice were returned to the study site before sunset. During the males' absence, the females and their nursing young were left confined to their respective couplets. On the tenth day of confinement, the arena hole was opened and the radiocollared mice and their respective families were allowed the opportunity to move freely about the site for the remainder of the 10-week experiment (Experiments 3.1 and 3.2). The mean age of firstborn litters in the population at the beginning and end of radiotracking for both seasons was 14.2 $\pm$ 0.9 (S.E.) and 42.0 $\pm$ 3.8 (S.E.) days, respectively.

Radiotelemetric monitoring of the tagged mice began on the first night following the opening of the arena hole. This allowed one day for the mouse to adjust to wearing the radiocollar before it was radiotracked. Hamley and Falls (1975) and others recommended that

radiocollared mice be monitored for any signs of abnormal behavior that might be a result of either the collaring procedure or of the collar itself. From preliminary observations of collared mice in the laboratory, I determined that a one-day adjustment period was sufficient. Herman (1977) also accepted a 24-hour familiarization period. During my preliminary observations, I noted that, for most mice, locomotory, grooming, and feeding behaviors were normal within 30 minutes after the radiocollar was attached. Monitoring involved surveying the site with a frequency modulated (FM) radio receiver once every two hours beginning shortly after sunset and continuing until shortly before sunrise. Due to differences in night length between the fall and spring (fall: $\bar{x}$ = 13.5 hrs; spring: $\bar{x}$ = 9.75 hrs), six radiolocations were possible during nights in the fall compared with only five nightly observations during the spring.

Locations of tagged mice were determined by a single observer who slowly searched the areas near the couplets and in the surrounding habitat at the study site. During the day, the collared mice and their families often occupied nests within particular couplets. Knowledge of these daytime nest positions offered a clue, at the start of each tracking period, of where to begin radio surveillance. These areas were the first ones scanned at the beginning of each tracking period. If the radio signal detected indicated that a collared mouse was present in a couplet, the nests located within the couplet (both arenas) were quietly checked. The use of a flashlight confirmed the presence of a collared mouse. The location of the collared mouse and, whenever possible, the location and identity of all other mice found in the nest-boxes were recorded. If a radiocollared mouse was not found

in a couplet and its radio signal was not detected in the area immediately surrounding its last known nest location, surveillance was carefully and quietly extended to the study site at-large. Searching continued until maximum signal strength was obtained. By reducing antenna gain, a successively smaller area of signal strength could be localized. At this point, scanning with a flashlight occasionally revealed the mouse moving slowly about in the grass. A position fix was recorded on a prepared map of the study site that was partitioned into 2 m squares. Any additional information regarding the collared mouse was recorded as notes on the site-maps. If the signal of a collared mouse was localized but the mouse was not directly observed, a description of the animal's likely refuge (if not in a nest) was noted. Also noted were descriptions of any encounters between a collared mouse and any other mice. In addition, at the beginning of each night of radiotracking, the air, temperature and sky conditions were noted. Minimum temperatures for each night were obtained from the National Weather Service office at Michigan State University.

At the end of every two-hour interval, the following data were collected and recorded: 1) location and identity of each collared male, and 2) the identity of each mouse found cohabiting with the collared male (if the collared male was found in a couplet).

Analysis

To answer the question concerned with male activity, several activity measures were examined. These included: 1) <u>frequency of movement</u> - the number of two-hour intervals during which a male changed locations/total two-hour intervals observed; 2) <u>distance moved</u> - distance moved/interval; and 3) <u>average step length</u> - distance moved/ number of intervals during which a male changed locations.

To answer the question concerning the likelihood of encounter between collared males and other mice, the following measures of social interaction were used. From records of nest checks at couplets where a collared mouse was found, the mice found cohabiting with a collared mouse were classified as either a family member or stranger. The percent of total observations in which a collared male was either alone, or cohabiting with a family member or stranger was determined. In addition, home range estimates of the collared mice were plotted from locations recorded on the site-maps.

The specific hypotheses tested here are:

1. Activity measures for fall and spring males are not expected to differ.
2. In both seasons, males will be more likely to move, and move farther, on nights when females are exhibiting post-parous estrus than on other nights.
3. The home ranges for fall and spring males are not expected to differ.

Comparisons of activity between seasons were made using t-tests. Within-male comparisons of activity during parturition periods and non-parturition periods were made using paired t-tests. Tests of the likelihood of males moving on nights during the parturition period versus non-parturition periods were made using a Wilcoxon matched-pairs signed-ranks test.

Results

The nine males in the fall 1981 (hereafter called Fall) were radiotracked for an average of ten nights each ($\bar{x}$ = 51 observations/

male) during the period from 20 October to 4 December. In the spring 1982 season (hereafter called Spring), seven males were radiotracked for an average of 12 nights each ($\bar{x}$ = 51 observations/male) from 27 April to 13 May. No collars were lost in either season. One collared male in the Fall was killed by a least weasel but the body and collar were recovered. Radiotracking of another Fall male was stopped prematurely due to an injury caused by a malfunctioning collar. There were no injuries or deaths directly attributable to the collars during the Spring. All of the collars were removed from the mice at the end of each radiotracking season.

Social Interactions

In both seasons, the males were most often found nesting or resting within a nest in a couplet (Table 4.1). Spring males were more

Table 4.1 Percent of total observations in which collared males occupied a couplet or a nest (if in a couplet).

	Occupation % (N obs)			
	Couplet		Nest (If in Couplet)	
	Fall 1981	Spring 1982	Fall 1981	Spring 1982
Present	87 (403)	72 (258)	93 (375)	98 (254)
Absent	13 (58)	28 (98)	7 (28)	2 (4)
Totals	100 (461)	100 (356)	100 (403)	100 (258)

likely than Fall males to be radiolocated outside of the couplet. Only rarely was a male observed between nests within an arena. On the few occasions when a male was visually observed in the field away from an

arena, the mouse was usually alone. However, on one occasion in the Spring, I was able to identify another mouse that was nearby; it was a 21-day-old son of the collared male. Both mice happened to be taking refuge in a small hole located approximately 15 m from the "home" couplet. Although juveniles were not radiotracked, some indication of their activity patterns was provided by checking nests in arenas occupied by collared males. Juveniles 16 days old or younger were almost always found in a nest, while older juveniles were found in nests less frequently. When present in couplets, both collared males and other mice were frequently found in the nest containing sunflower seeds.

In both seasons, males were more likely to be found sharing a couplet with family member than with a stranger, although the male was usually alone in a nest (Table 4.2). Family members consisted of the

Table 4.2 Percent of total observations in which collared males were alone or cohabiting with other mice in a couplet or in a nest (if in a couplet).

	Cohabitation Condition % (N obs)			
	Male in Couplet		Male in Nest (If in Couplet)	
	Fall 1981	Spring 1982	Fall 1981	Spring 1982
With Family	54 (217)	63 (161)	19 (72)	30 (75)
With Stranger	6 (24)	1 (3)	3 (11)	0 (1)
With Family & Stranger	3 (14)	0 (0)	0 (0)	0 (0)
Alone	37 (148)	36 (94)	78 (292)	70 (178)
Totals	100 (403)	100 (285)	100 (375)	100 (292)

male's mate and her offspring. A male was found with a stranger in the same couplet on 27 observations (Table 4.2: Fall = 24; Spring = 3) with either a lone adult, or an adult with offspring present. Collared males were never found with only a strange juvenile, and only six observations were with other adult males. The six male-male encounters occurred on two nights between two males in the Fall (Mouse D and I; Figure 4.2). On these two nights, a strange collared male (I) was found in an arena shared by a formerly-collared male (D) and D's mate and offspring. There was evidence of severe wounding on the head and belly of the resident male (D). On several observations during these two nights, the intruder male was found in the same nest with D's mate and juvenile offspring. On these observations, D was found alone in a separate nest. On the third day following the initial observed encounter between the two males, D moved 40 m south to an adjacent couplet. The intruder male maintained D's original mate as a consort for an additional two weeks until the end of the experiment.

Twenty-one observations (78%) of male-stranger encounters were between a collared male and an adult female. On 13 of these observations, the female had either just given birth on that day or the previous night. Males were frequently found in the same couplet with a postparous female (either his original mate or a stranger) even though, in some cases, the male had never before been observed in that couplet.

Activity Patterns

General

In the Fall, collared males changed locations, on the average, once out of every four observations, moving nearly 26 m at a time (Table 4.3). Spring males had a higher frequency of movement than Fall

Table 4.3 Mean activity measures of radiotracked males.

Activity	Season						Difference Between Seasons (t)
	Fall 1981			Spring 1982			
	$\bar{x}$	S.E.	Range	$\bar{x}$	S.E.	Range	
Frequency of movement (moves/ interval)	0.25	± 0.08	0.00 to 0.60	0.37	± 0.08	0.00 to 0.64	1.10 NS
Distance Moved (m/interval)	8.34	± 2.30	1.83 to 17.50	9.34	± 1.03	6.77 to 13.70	0.37 NS
Average Step Length (m)	25.72	+ 2.75	18.33 to 39.20	26.07	+ 6.56	13.54 to 57.50	0.05 NS

males but the difference was not significant ($t = 1.10$; $df = 14$; $p > 0.10$). There was also no difference in the average step length between Spring and Fall males ($t = 0.05$; $df = 14$; $p > 0.25$). When distance traveled is measured as meters moved/2-hr interval (to correct for differences in night length between Fall and Spring nights), one finds that, again, Fall males moved no further than Spring males ($t = 0.37$; $df = 14$; $p > 0.25$).

Figures 4.2a-c illustrate the space use by the nine Fall and seven Spring males. Males typically restricted their movements between neighboring couplets. Males often centered their activity around a couplet that served as a diurnal refuge.

Activity areas are estimated by joining peripheral positions by a minimum number of straight lines and measuring the enclosed area (Madison, 1978). The average activity area for mice that moved was 0.077 ± 0.03 hectares for Fall males and 0.112 ± 0.02 hectares for the seven Spring males. Two males in the Fall and one male in the Spring were never observed outside of their home couplet.

I detected no clear pattern of weather influence on activity patterns. Mice appeared to be just as active on cold, snowy nights in the Fall as they were on mild, dry nights in the Spring. The average low temperatures on nights during the Fall and Spring radiotracking periods were $39.0 \pm 8.1^{o}C$ and $45.4 \pm 2.3^{o}C$, respectively.

<u>During parturition periods</u>

Males from both seasons were more likely to move on nights during periods when neighboring females were in parturition than on nights when no parturition occurred (Figures 4.2a-b; Wilcoxon matched-pairs signed-ranks test, $p < 0.05$). Males in the Fall moved significantly

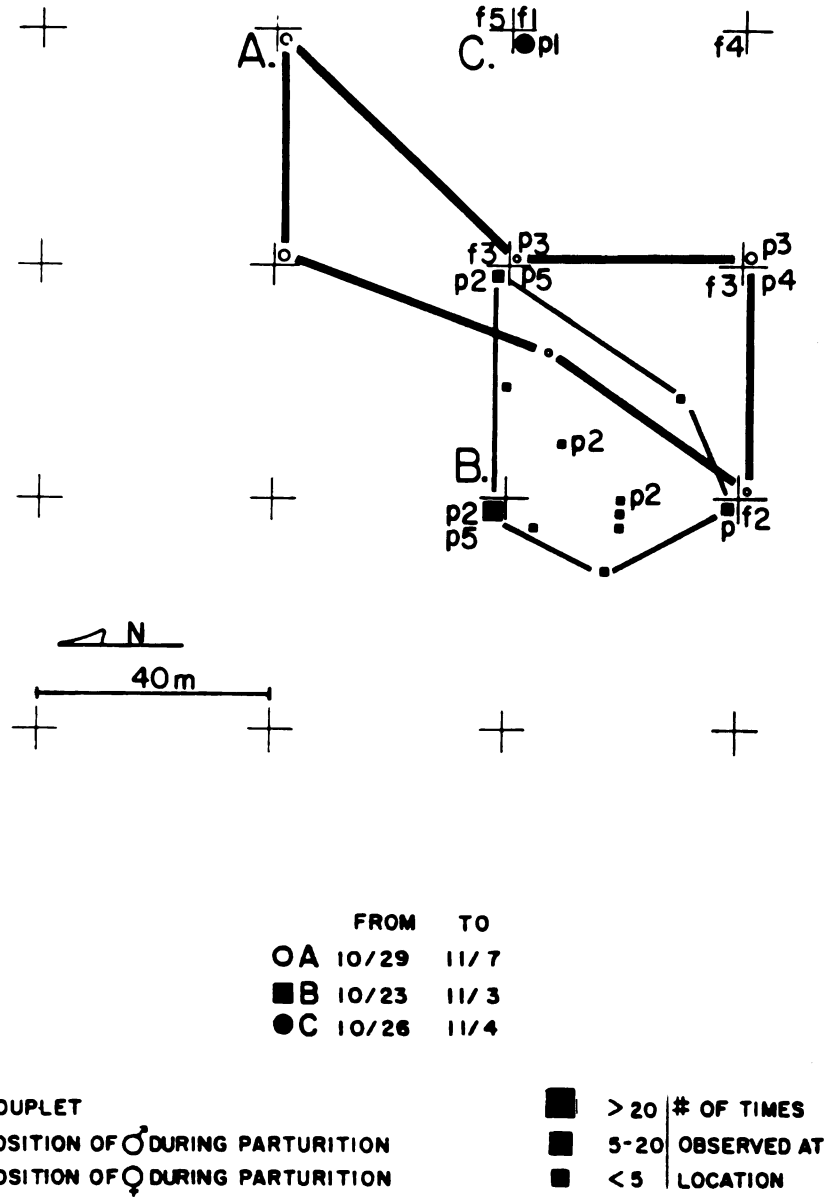


Figure 4.2a Positions of 3 collars males obtained during 2 weeks of radiotracking in the Fall 1981. The positions are superimposed on a map of the mouse cities and indicate the relative frequency of observation at any given location as well as the position of males relative to the position of neighboring parturient females (see text for explanation).

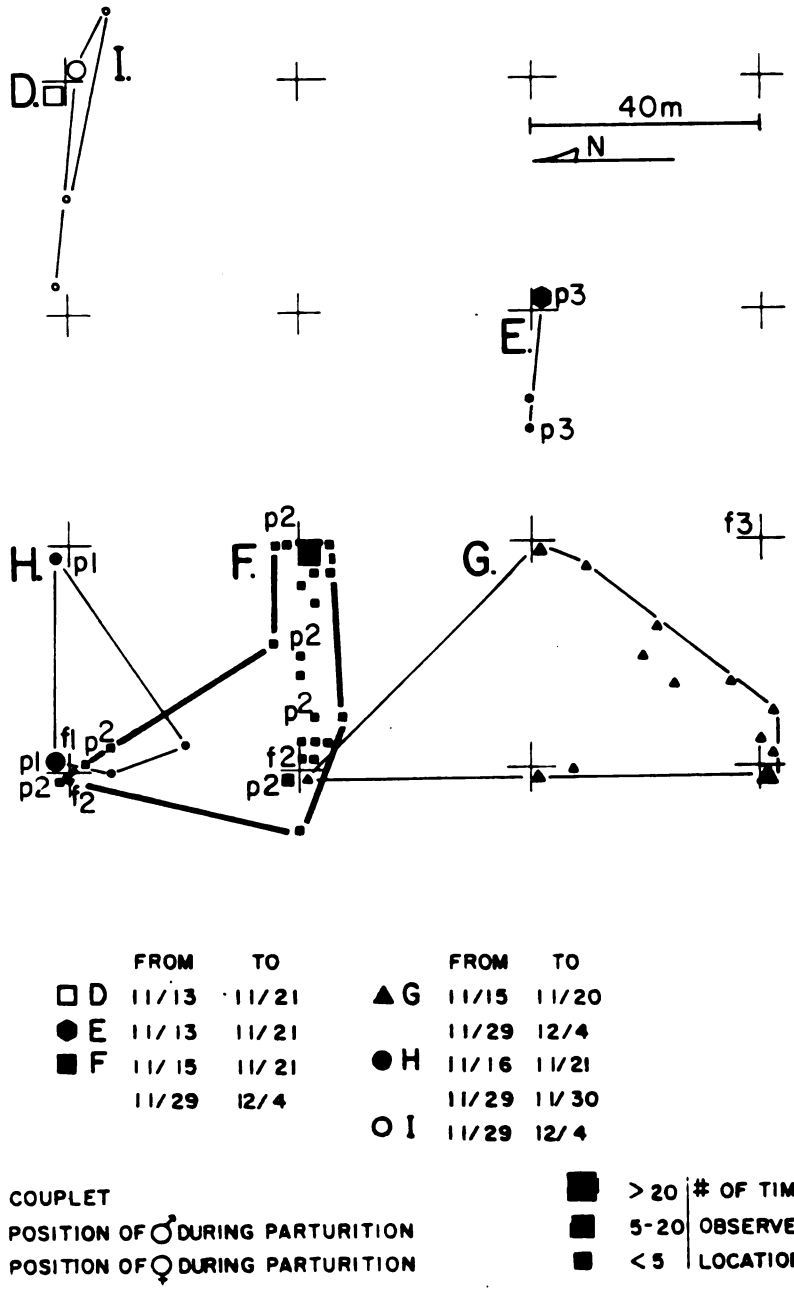


Figure 4.2b Positions of 5 collared males obtained during 3 weeks of radiotracking in the Fall 1981. The positions are superimposed on a map of the mouse cities and indicate the relative frequency of observation at any given location as well as the position of males relative to the position of neighboring parturient female (see text for explanation).

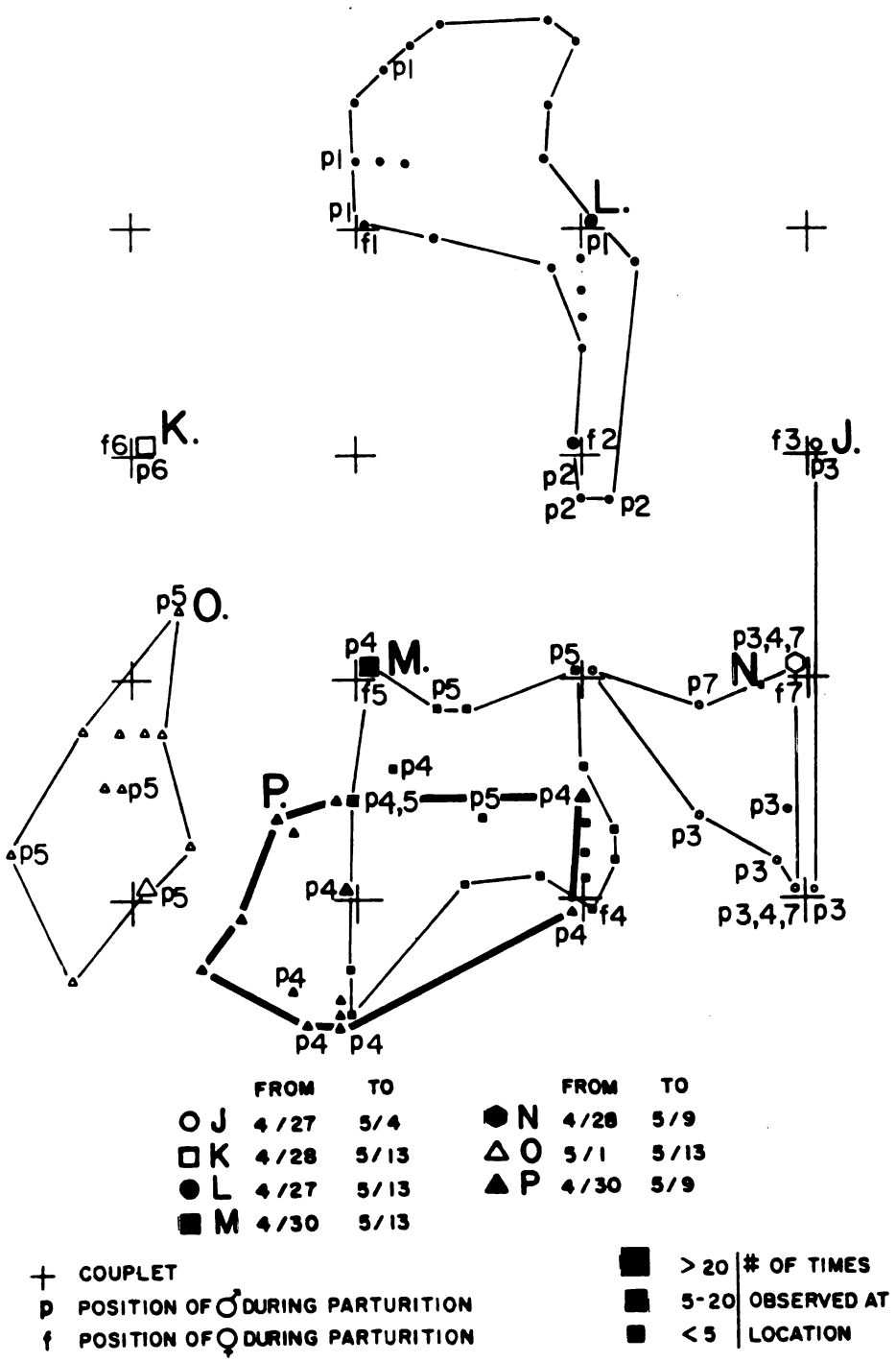


Figure 4.2c Positions of 7 collared males obtained during 2 weeks of radiotracking in the Spring 1982. The positions are superimposed on a map of the mouse cities and indicate the relative frequency of observation at any given location as well as the position of males relative to parturient females (see text for explanation.)

greater distances on nights during parturition periods than during nights of non-parturition periods (Figures 3a, b; Table 4.4; $t = 3.32$; $df = 3$; $p < 0.05$). Males in the Spring also moved greater distances during nights of parturition periods but not significantly so ($t = 1.86$; $df = 5$; $0.10 > p > 0.05$).

Discussion

Social Interactions

The results of this experiment indicate that a considerable degree of familial cohesion exists among free-ranging *P. m. bairdi* during their nocturnal activities. These findings are in close agreement with results of diurnal nest-box censusing reported in Experiments 3.1 and 3.2 (Chapter 3), and in King (1983). Males from both seasons spent a majority of time each night in a couplet. However, spring males were more likely than fall males to be absent from a couplet (Table 4.1). On nearly 60% of all Spring observations, males were found sharing a couplet with at least one family member (Table 4.3). The presence of family members in a couplet could have attracted a male to the couplet and maintained his residency there. A male that shares a couplet with his family may be also assist his mate in parental care of their offspring. One fall male nested with his 12-day old offspring for two nights following the permanent disappearance of his mate. Paternal care has been observed in California mice, *Peromyscus californicus parasiticus* (Dudley, 1974) and in a laboratory-reared deer mice (Horner, 1947); however, observations of direct attentiveness by males towards their offspring in the present study were rare. I typically found a male and his family in separate nests or even separate arenas within a couplet. This was true especially when females were nursing

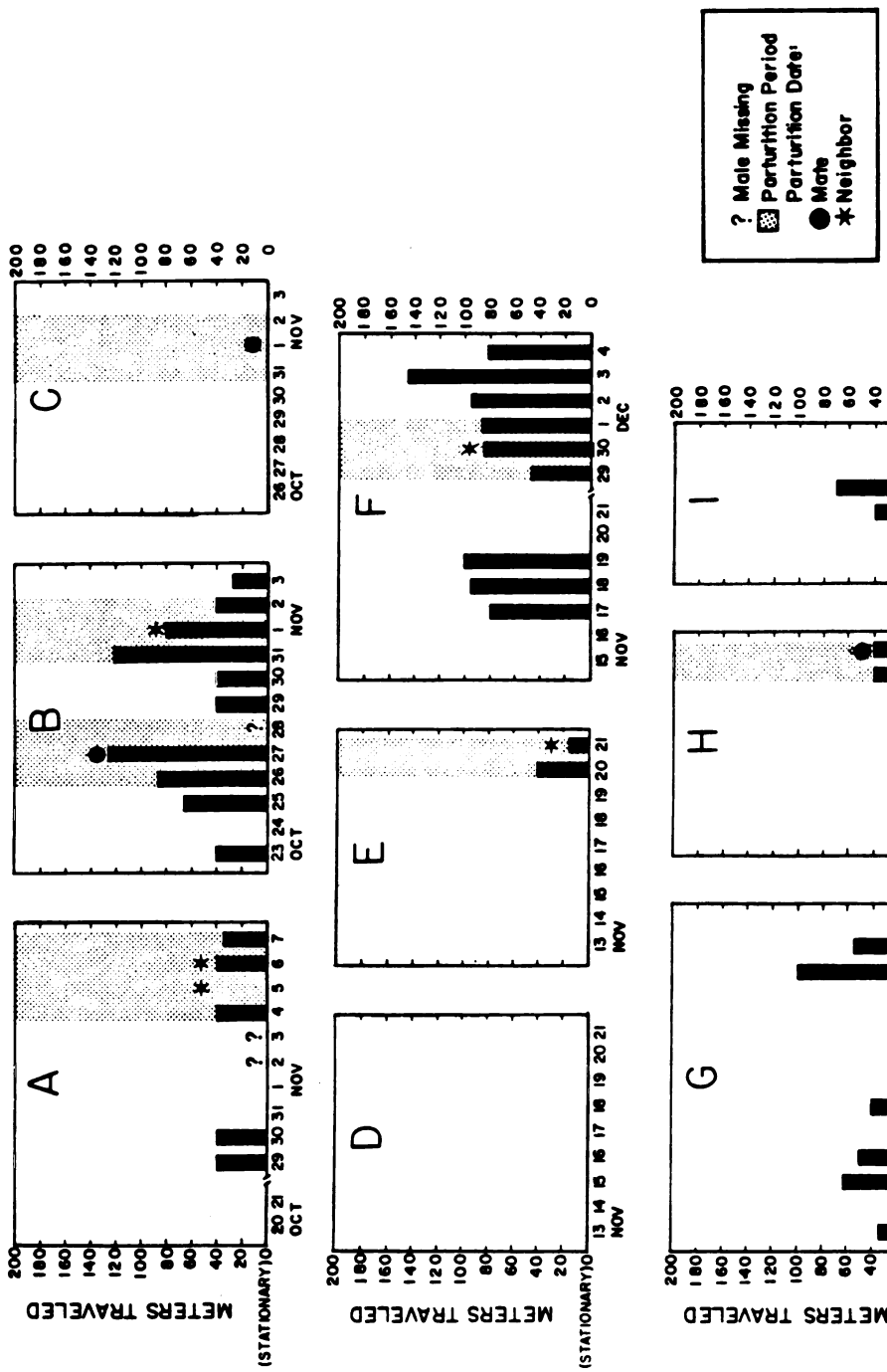


Figure 4.3a Total nightly distances traveled by radiocollared males in the Fall 1981. The graphs illustrate the distances traveled by males during the parturition and non-parturition periods of neighboring females.

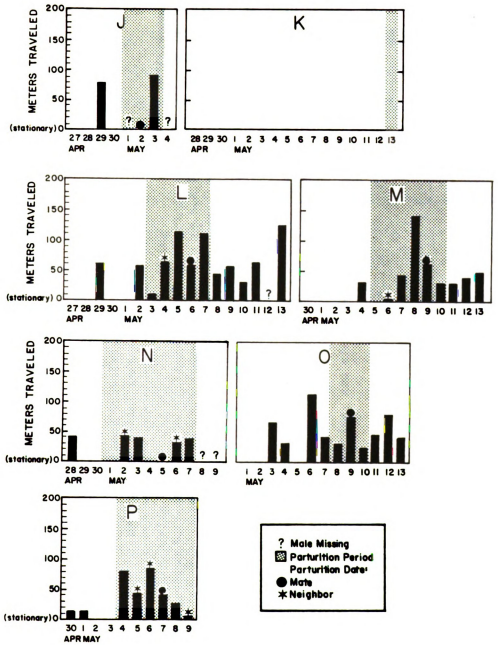


Figure 4.3b Total nightly distances traveled by radiocollared males in the Spring 1982. The graphs illustrate the distances traveled by males during the parturition and non-parturition periods of neighboring females.

Table 4.4 Relationship between time of parturition by closely neighboring females and activity of collared males.

Season	Distance Traveled By Collared Males[a] (m/interval)						Difference Between Periods
	Nights During Parturition Periods[b]			Nights During Non-Parturition Periods			
	N_{mice}	$\bar{x}$	(± S.E.)	N_{mice}	$\bar{x}$	(± S.E.)	t[c]
Fall 1981	4	15.90	(4.21)	4	6.86	(3.10)	3.32 *
Spring 1982	6	15.15	(2.40)	6	8.19	(2.30)	1.86 NS

[a]Includes only males that moved during both periods.

[b]3-day period consisting of one night before, during, and after the date of parturition.

[c]Paired t-test.

*$p < 0.05$ (One-tailed).

young pups. The apparent avoidance between adult males and adult females with offspring is a pattern observed during both diurnal nest-box censusing (Experiment 3.1, 3.2, Chapter 3; King, 1983; Howard, 1949) and nocturnal monitoring. Hill (1977) suggested that dispersion patterns observed in natural populations of Peromyscus result more from mutual avoidance than from aggression. If males are providing parental care for their offspring during nocturnal periods, it probably occurs during brief encounters within the nests. Most encounters within nests were between an adult male and his mate. Rarely was an adult male found in a nest with only his offspring.

No aggression was detected during observed encounters between family members. I am not aware of any published reports of observed aggression between family members in natural populations of Peromyscus, although aggression between mothers and their offspring has been observed in a laboratory study by Savidge (1974). Under the conditions of this study, Savidge suggested that some mothers attacked their offspring after he introduced the young to the mothers' cage, while other mothers did not. Savidge also suggested that differences in aggressiveness between mothers might explain observed differences in the rates of departure of their offspring from the natal cage. He hypothesized that offspring of "aggressive" mothers would depart the natal cage at a higher rate than offspring of "non-aggressive" mothers. He based his classification of aggressiveness on whether or not females attacked strange juveniles. A test of his hypothesis revealed that juveniles with "aggressive" mothers departed from the natal cage at a higher rate than those with "non-aggressive" mothers, although he did

not report any observations of aggression between mothers and their offspring.

Most demonstrations of aggression under laboratory conditions have been observed between non-family members (Rowley and Christian, 1976; Ayer and Whitsett, 1980; Gleason, et al., 1981; Whitsett, et al., 1979). Halpin (1981) reached an opposite conclusion in a study of interactions between parents and their own offspring. She reported "an almost complete lack of aggression between adults and their own young." Halpin went on to suggest that parental aggression may be more prevalent under field conditions after the birth of a second litter, however, I found no field evidence of parental aggression towards firstborn juveniles either before or after the birth of a second litter.

Males were found in a couplet with only a stranger on just 7% of all observations (Table 4.2). In the majority of these observations, the male was found with a lone adult female, or an adult female with her offspring present. I never observed a male in a couplet with only a strange juvenile. Encounters with a strange adult female usually occurred on nights during her period of parturition and post-partum estrus. Interactions of this type were also revealed by radiotelemetry for meadow voles, Microtus pennsylvanicus (Madison, 1978, 1980b). Madison reported that radiocollared males were significantly more likely to overlap in space with neighboring males and females when females were in estrus than when they were not in estrus. In the present study, some observations of couplet sharing between a male and an adult female revealed that the male was visiting the couplet for the first time. This suggests interesting questions regarding the

mechanisms by which males detect the presence of estrous or pregnant females. It is likely that males, in their wanderings between couplets, are attracted to cues provided by an estrous or pregnant female. Chemical signals produced by female rodents are probably the most important cues for attracting males to females (see reviews by Aron, 1979; Brown, 1979; Gosling, 1982). Moore (1962, in Bronson, 1979) demonstrated that female P. maniculatus produce substances that attract males. In mice, the attractiveness of female urine increases during estrus or pregnancy (Bellamy and Davies, 1971; Davies and Bellamy, 1972). Whether the male is responding primarily to cues localized at the females' home couplet, or distributed generally in the field surrounding the couplet, is not known. Although adult females were not radiotracked, their habits could sometimes be inferred from checking nests in couplets occupied by collared males. Females spend some portion of each night wandering in the field away from the couplets as indicated by occasional trap captures. I don't know the amount of space used by an average adult female, but if it is similar to that of a male, she has the opportunity to release olfactory signals (in her urine or other secretions) over a wide area surrounding her home couplet. The attractiveness of urine from estrous or pregnant females to males could explain the observed cohabitation of males with females during their parturition periods.

Only six male-stranger encounters were between two males. These encounters provided the only evidence (p. 172) of intraspecific aggression between two mice. Although there have been reports of observed male-male aggression among laboratory reared Peromyscus (Healey, 1967; Ayer and Whitsett, 1980), no one has reported aggressive

encounters in a natural, unconfined population. The likelihood of male-male aggression is probably rare in natural populations because male-male interactions are similarly infrequent. Data reported from nest-box studies indicate that, during breeding seasons, same-sex cohabitations are rare (Nicholson, 1941; Terman, 1961; King, 1983).

Although males were frequently found in a couplet shared by family members, males were often alone in couplets (Table 4.2). Therefore, social attraction among family members is not necessary to explain the attractiveness of couplets to adult males. Males observed in otherwise unoccupied couplets were frequently found in the nest containing sunflower seeds, and I assumed the mice were feeding. It appears that even an unoccupied couplet, with its supplemental food and refuge sites, is attractive to free-ranging males. In fact, three males (two Fall, one Spring) were never observed outside of their home couplet during the radiotracking period.

Although males were radiolocated at locations away from a couplet on 156 observations (Table 4.1), I rarely visually observed the mice. On one occasion, however, I observed a male and his weanling son enter a refuge together. Other field observations indicate that juveniles may be attracted to the father. Howard (1949) reported finding a father and his four offspring (P. m. bairdi) in a live trap 300 ft. from their home nest-box. Howard suggested that juvenile P. m. bairdi follow their parents about in the process of becoming familiar with the parents' home range. In a laboratory investigation of possible dispersal mechanisms in P. m. bairdi, Savidge (1974) found that weanling juveniles are attracted to the father.

Activity Patterns

Although radiotelemetry studies have contributed greatly to our understanding of the activity patterns of free-ranging microtines (e.g. Banks, *et al.*, 1974; Brooks and Banks, 1971; Herman, 1977; Madison, 1978, 1980b; Webster and Brooks, 1981a) and *P. leucopus* (e.g. Madison, 1977; Mineau and Madison, 1977; B. Ormiston, unpub. obs.), little is known about the movements of free-ranging *P. m. bairdi*. In this study, males from both seasons typically made just over one move per night. The average distance traveled per move was the same for males from both seasons (Table 4.3). No mouse moved further than 145 m on any given night. Based on live-trap records and a knowledge of nest-box homesites, Howard (1949) reported maximum nightly linear movements ranging from 15 to 107 m. Dice and Howard (1951 reported that *P. m. bairdi* seldom travel more than 123 m in a straight line from their homesites. These distances are comparable to the nightly values for cumulative distances traveled in this study (Figures 4.3a, b). Most mice moved less than 100 m on any given night.

Males were just as likely to move on nights at the beginning of the tracking period as they were on any other nights (Figures 3a, b). Similarly, there was no discernible pattern of hourly movement on any given night. Males could be found moving at any hour of the night, from shortly after sunset until shortly before sunrise. Males from both seasons were more likely to move and to move farther on nights during periods when neighboring adult females were in parturition than on nights when no parturition occurred (Table 4.4; Figures 4.3a, b). These results suggest that males actively search for females, and this search intensifies on nights during parturition periods of neighboring

females. Female P. maniculatus in estrus (and presumably, post-partum estrus) are known to produce signalling pheromones that are attractive to adult males (Moore, 1962; from Bronson, 1979; Moore, 1965). A male probably detects these signalling odors during his wanderings away from his nest and, upon detecting the odor, increases his level of activity in search of the estrous female. Curiously, some males that shared a couplet with a mate on the night of her parturition also moved far on that night (mice B, H, and L: Figure 4.2a, b). I would expect a male to remain in close proximity to his mate during the time she was in post-partum estrus to insure his chance of acquiring an exclusive mating with her. Dewsbury (1979, 1982) reported that female P. m. bairdi in cycling estrus require more than one ejaculatory series from a male in order to maximize probability of pregnancy. However, if the female is in post-partum estrus, a single ejaculatory series is sufficient for maximum probability of pregnancy. Thus, if a male wanted to insure a fertile copulation with a post-partum estrous female, only one ejaculation series is required. Remaining close by the female would not necessarily represent any additional reproductive benefit for either the male or female. This could explain the behavior of males B and H (Figures 2a, b) who were found only once in the same arena with their mates on the night of parturition and were absent from them during the remainder of that night's observation. From Dewsbury's findings, I predict that males should spend more time in close vicinity of cycling estrous females than with post-partum estrous females.

In addition to searching behavior on the part of males, estrous females could also be active in search for males. Doty (1972a,b, 1973) reported that male urine can act as an attractant to estrous female P.

m. bairdi. Post-partum lactating females are known to spend considerable time away from the nest (P. leucopus: Hill, 1972; Harland and Millar, 1980) and would, therefore, be likely to encounter other mice. Although all observed encounters between post-partum females and males took place in her home couplet, it is possible for a male and female to encounter each other while both were wandering away from the nest. Further work with telemetry systems under field conditions is required to learn more about the dynamics of mating behavior of P. m. bairdi. Reserach is currently underway to develop a sensitive electronic tagging system that can be used to monitor the activity of individual mice at a nest (R. Hill, pers. comm.). This recording system could be used to gain considerable information on patterns of nest visitation among reproductively active mice.

In the present study, radiotracking methods revealed information on patterns of activity, space utilization, and nest cohabitation among free-ranging adult male P. m. bairdi that would have been difficult or impossible to collect with conventional live-trapping methods. However, all studies which utilize radiotelemetry can be criticized on several grounds (see also Literature Review). The most significant problem pertains to the assessment of the effect of the radiotransmitters upon the animal's behavior (Brooks and Banks, 1971; see also Hamley and Falls, 1975; Webster and Brooks, 1980). In this study, I relied mostly on subjective criteria to evaluate possible transmitter related interference of normal behavior patterns. I detected no noticeable effects of radiocollars on grooming or feeding behaviors in mice confined in the laboratory. Although a radiocollar fit snugly around the mouse's neck, feeding behavior did not appear to be

disturbed. In the food supplement nest in the field, collared mice were frequently seen feeding normally on sunflower seeds. Nevertheless, I was concerned that the stress of carrying a 2 g collar around might result in an energy deficit and a loss of weight in the mouse. I compared body weights of mice before and after radiotracking and discovered that post-tracking weights were within 1 g of pre-tracking weights. One exception was a mouse which lost 2 g in body weight (19.0 g to 17.0 g). If wearing a radiocollar caused an energy deficit in the mice, body weights could have been maintained in one of two ways. First, a collared mouse could have responded to the burden of carrying around extra weight by reducing his activity and restricting his use of space to the close vicinity of his home couplet. Secondly, a collared mouse could feed more, in which case he could stay in the couplet and feed on the supplemental sunflower seeds, or he could forage widely in search of other food. In this study and others (Howard, 1949; Howard and Evans, 1961), mice stored large caches of wild weed seeds, suggesting that mice were spending time foraging away from the nest and not restricting their intake of food to sunflower seeds. Although mice may have been foraging for food, a comparison of size of activity areas used by males in the present study with home ranges measured by Blair (1940) suggests that mice in the present study were actually restricting their foraging to areas near their home couplet (Figures 2a-c). Blair's estimate of male home range size is 2.5 to 4 times the average area of activity recorded for mice radiotracked in the spring and fall, respectively (see Results). Although radiocollars could be restricting normal activity, I believe the disparity in estimates of space use can be explained by Blair's use of live traps over a longer

period, and by recognizing that mice in the present study were newly introduced to the study site. Blair's mice were natural residents in a completely natural field. The study site of the present study was also not considered natural habitat for P. m. bairdi in south-central Michigan (King, 1983).

Despite potential radiocollar interference and restrictions in the sampling regime (e.g. sampling only once every two hours), I believe that radiotracking, in conjunction with nest-box censusing, was a valid technique for measuring the likelihood of encounter between adult males and other mice in the population. The results of this study indicate that: 1) adult males restricted their movements to areas between their home couplet and neighboring couplets; 2) males were more likely to move, and move farther, on nights during parturition periods than on nights during non-parturition periods; 3) males spent a majority of each night in the same couplet with family members and were more likely to be found sharing a nest with a relative than with a stranger; and 4) aggression between adult males and other mice was rare; a single observation of aggression occurred between two adult males.

GENERAL DISCUSSION

Very few topics in field biology offer more challenge to the investigator than dispersal. Dispersal is variously described in the literature on small mammals. It has been regarded as immigration or emigration (Lidicker, 1962, 1975), disappearance (Beacham, 1979; Pfeiffer, 1982), searching behavior (King, 1983), exploratory migration (Mather, 1981), long-distance movement or travel (Myllymäki, 1977; Watts, 1970), "leaving the area" (Fairbairn, 1978a), or simply, movement (Christian and Davis, 1964; Grant, 1978, Fairbairn, 1978a). Frequently, some of these words are used interchangeably even in the same study. Furthermore, dispersal can be defined as, among other things, the movements of an animal from a source (Brown, 1975), or the movement of an animal from its place of birth to a place where it breeds (Howard, 1960). Adding to this inconsistency is the problem of measuring the movements of animals in the field. Typically, dispersal movements among small, secretive animals are inferred from data collected with live-trapping methods. In many live-trap studies, a disperser is regarded as a marked individual that is captured in a location some distance away from its former area of residence. Unfortunately, the criteria used to define a disperser vary from one study to the next; therefore, it is hardly surprising to find so many descriptions of dispersal (see Literature Review, Chapter 1).

A second challenge to a dispersal biologist is the determination of a cause or causes for dispersal. In live-trapping studies, besides knowing the length and the direction of movement made by a disperser, very little is known regarding the process of the dispersal event. Nonetheless, a knowledge of the dispersers' sex, age, weight, genotype,

and reproductive condition at the time of capture provides some clue to understanding the causes and mechanisms of dispersal. For example, in an annually cycling species, such as Peromyscus, dispersers are usually, but not always, young, lightweight individuals of either sex which may, or may not, be sexually mature. One explanation for the cause of dispersal of these individuals is the response of young individuals to aggression and social pressure by resident adults (e.g. Fairbairn, 1978a; Petticrew and Sadlier, 1974). Frequently, only one, or at most, a few causes are ascribed to dispersal in any particular study because many investigators disregard the considerable variation in the characteristics of dispersers. For instance, there are many examples in the literature of attempts made by authors to identify from a varied sample of dispersers, a predominant or "mean disperser" - for example, a young, sexually mature juvenile - and then propose a cause for its dispersal. As an example, it may be suggested that because this disperser is sexually active, it is dispersing to search for a mate, or to avoid mate competition with older resident adults. While these explanations may apply to the sexually mature disperser, what about those dispersers that are sexually inactive? Perhaps these other dispersers are not moving to find a mate but, instead, are moving to secure some other resource such as food. Often, these other dispersers and the reasons behind these different movements are ignored.

Certainly, the variation in disperser characteristics suggests that individuals move or disperse for many reasons. Why, then, is there an apparent reluctance on the part of many investigators to propose multiple explanations for dispersal? Part of the reason may be that it is intuitively appealing to expect a universal cause for the

phenomenon. Secondly, and more importantly, few experiments are designed to identify and experimentally examine, the ecological variables, such as resource availability, that could influence dispersal.

An individual's decision to move or disperse depends on its unique perception of the spatial and temporal availability of important resources such as mates, food, shelter, etc. Although few investigators would deny the important influence that these ecological variables may have on dispersal, these factors have been, nevertheless, difficult to assess and control in the field. Often, this problem can lead to fortuitous interpretations of the causes of dispersal. For example, in her study of P. maniculatus, Fairbairn (1978a) argued that the cause of dispersal in lightweight subordinate males varied seasonally. She believed that in one season these individuals dispersed as a result of competition with larger, dominant males over the availability of receptive mates. In another season, she believed that this same type of individual dispersed due to local limitations in the supply of food and nesting sites. Because these variables were not controlled in each season, it is diffuclt to be certain, for instance, that food supply was limited in one season and not the other. Obviously, if the supply of mates and food were both limited in the same season, dispersal could be attributed to either one or both.

In addition to a weak knowledge of how resource availability affects dispersal, in many studies little is also known about the social processes involved. Although Anderson (1980) has said that "dispersal is a social, rather than an individual, process," the social context under which dispersal occurs is often ignored or misinter-

preted. Some investigators have argued that juvenile dispersers may be forced out of their natal area by their parents. Although behavioral interactions between parents and their offspring are certain to influence the offspring's decision to disperse (Savidge, 1974), parental aggression is probably rare under natural field conditions (Terman, 1961). I doubt that many of the investigators who support this aggression argument understand the true nature of the behavioral interactions that occur between adults and juveniles in the field. Most of the evidence for juvenile-directed adult aggression is derived from laboratory studies in which adults are exclusively paired with unrelated juveniles. This may be the wrong social context for judging whether aggression in adults can explain the dispersal of juveniles from their natal area. For instance, field evidence suggests that prior to natal dispersal, juvenile P. m. bairdi are likely to be found with their parents and not with unrelated adults (Howard, 1949; King, 1983; Chapter 4). Furthermore, the likelihood of adult aggression toward their own offspring is low (Halpin, 1981). These results, therefore, challenge the importance and relevance of adult aggression as a catalyst for juvenile dispersal, at least for P. maniculatus. This example illustrates the value of knowing something about the early social history of the disperser (Bekoff, 1977, 1981), which is easier to obtain in nest-box studies because the familial composition of the population can be determined. For live-trap studies, on the other hand, the social history of the dispersers is a "black box."

To summarize, I see four limitations in the way that dispersal has been studied in the past. The first is that operational definitions of dispersal are so varied that it becomes difficult to interpret what

kinds of movements are being measured. Animals move for many reasons. Secondly, very little is known about the spatial and temporal distribution of resources that may affect an individual's movement patterns. Third, an understanding of dispersal requires that we attempt to take into account the social context under which animals disperse, something that has been difficult to do. Fourth, in the past, many investigators have relied almost exclusively on the visible characteristics of dispersers caught in traps to infer the causes of dispersal. Looking for the causes of dispersal in this manner can be likened to someone searching for lost keys under a streetlight, not because they were lost there, but because that is where the light is. Investigators have looked at the circumstantial evidence of age, weight, sex, reproductive condition of the dispersers and suggested probable causes for the dispersal. What is needed though are more attempts to identify and experimentally control features of the ecological and social stage from which individuals disperse.

In the past 5 years descriptive studies have been replaced by experimentation. In these studies particular attention has been placed on controlling certain variables known to be important in dispersal, and manipulating others. Manipulations have included the provision of supplemental food (Desy and Thompson, 1983; Gilbert and Krebs, 1981; Taitt, 1981), alteration of sex ratios (Redfield et al., 1978), and provisions of extra refuges (Taitt et al., 1981). The importance of aggressive behavior as a mechanism for promoting dispersal has been examined by using exogenous hormone treatments (Krebs et al., 1977; Taitt and Krebs, 1982). The endocrinological cause of natal dispersal

in ground squirrels was also examined with the aid of gonadal steroid treatments (Holekamp, 1982).

In many studies, the potential influences of environmental features and individual differences in resource requirement on dispersal were considered. Nonetheless, limitations in the experimental designs need to be overcome before we can understand what effect the manipulations in behavior or resource availability have on dispersal. For example, Taitt and Krebs (1982) compared the rates of immigration of voles onto a grid containing "aggressive-females" (Testosterone-treated) and several control grids. Immigration of females onto the testosterone grid was higher than it was on either control grid. These results, however, are difficult to interpret because the testosterone and control grids also differed quantitatively with respect to vegetation and cover, which are also known to influence spacing behavior (Taitt et al., 1981).

Many variables have been associated with dispersal, including cover or shelter, nesting sites, nutrition, population density, sex, age, reproductive condition, competition, and predation. In most live-trap studies, few of these independent variables are experimentally controlled in contrast to some success in enclosure studies (e.g. Gipps and Jewell, 1979). Unfortunately, dispersal in fenced enclosures is restricted (cf. Riggs, 1979).

Although I criticized the practice of hypothesizing one cause of dispersal, I felt justified to test only the sexual search hypothesis because I partially controlled resource availability and other variables known to influence dispersal. Peromyscus m. bairdi readily uses nest-boxes (Howard, 1949; Dice and Howard, 1951; King, 1983) which

allowed me to control the availability of shelter and nest sites and exert some control on predation. Furthermore, by introducing a known number of established breeding pairs into the arenas I was able to control initial demographic features of the populations studied. Because P. m. bairdi readily ate sunflower seeds, I was also able to control the quantity of food available to the mice.

The lack of mortality at the nest suggests that disappearing juveniles dispersed from their natal area. Natal dispersal was most likely to occur among juveniles that had recently become pubertal. By treating mice with the anti-gonadal hormone melatonin, I was able to retard pubertal development and delay natal dispersal in the treated mice. If mice disperse in search of a resource that is limited in their area of birth (e.g. Dice and Howard, 1951), then many of these resources were at least partially controlled in the present study: nesting sites, quantities of food, and shelter from predators. One resource that I did not control was mate availability.

In the small family groups of mice that are characteristic of P. m. bairdi (Howard, 1949; King, 1983; present study), juveniles rarely mate with siblings or their parents. For example, in Howard's study, only 4 - 10% of the litters observed could have been produced by matings between siblings or between parents and offspring. Inbreeding avoidance among siblings has also been observed in the laboratory. Hill (1974) reported that sibling pairs of P. m. bairdi had lower reproduction and reached reproductive age later than unrelated pairs. Parent-offspring matings are also uncommon but probably occur more often than matings between siblings (Haigh, 1983, Howard, 1949, Spevak, 1981).

The infrequency of consanguineous matings could be attributed to reproductive inhibition among young deermice by their parents. Deermice mothers can completely inhibit reproduction in their daughters if they are housed together in the same cage (Haigh, 1983). Pubertal development in the present study was delayed by melatonin treatment but not by the presence of the mother. Perhaps parental influences may inhibit reproductive success of juveniles even though parents do not appear to delay gonadal development in their offspring. Clearly, more research is needed to determine how parent-offspring social interactions in the field influence reproductive competence in young mice.

Juveniles may have little opportunity to mate if they remain in their family group. Therefore, it behooves sexually maturing juveniles to leave their natal area in order to reproduce. In the present study, departure from the natal couplet for other resources was probably not the cause of dispersal. Nesting sites, refugia, food, and water were in ample supply, which leaves potential mates as the most limited resource at the natal couplet.

Juvenile dispersal may be based upon the individual's gonadal maturation and perception of sexually attractice stimuli in the environment surrounding the natal area. Various odors, particularly those found in urine, are known to be attractive to the opposite sex (e.g. see review by Aron, 1979), and may explain why mice leave their natal nest site. It is certainly plausible that these and other social signals may be found in excretory markings located throughout the individual's environment. These signals could be detected when 2-week-old juveniles begin to explore the area immediately surrounding their natal nest (Chapter 4; Howard, 1949; Layne, 1968). General

activity increases a few days after eye-opening (R. Hill, pers. comm.), and juveniles may make excursions from their nest by following their parents (Howard, 1949; Chapter 4). By the age of puberty, they have acquired considerable information regarding their environment, including sexually attractive stimuli and other social signals (Mather, 1981).

Perhaps the absence of social signals from the environment could explain why steroid-treated mice failed to exhibit any more movement than controls in the fall experiment (Experiment 3.2). In the absence of sexually attractive stimuli, perhaps no level of gonadal steroids is sufficient to stimulate sexual searching in treated mice. Indeed, sexually attractive stimuli may have been reduced in the fall experiment because fewer juveniles were recruited into the reproductively active portion of the population than were spring and summer-born mice. Unfortunately, it was impossible to assess or directly control the level of sexually attractive stimuli. The effect that the levels of sexual stimuli have on the rate of dispersal in sexualy active individuals could be tested by manipulating the proportion of sexually mature males and cycling females in the population. In the fall, an increase in the number of sexually mature mice should increase the rate of dispersal among steroid-treated juveniles. A decrease in the level of sexually active mice, on the other hand, should reduce the rate of movement.

Because odors may provide the most information to an individual regarding the location and reproductive condition of potential mates (e.g. Eisenberg and Kleiman, 1972), further tests of the sexual search hypothesis could involve manipulations of the olfactory capabilities in

pre-pubertal mice. Spring and summer-born mice that are made anosmic should be less likely to disperse from their natal site at puberty than untreated individuals.

Sexually attractive signals may not have been the only stimuli important for the departure of pubertal juveniles from the natal area. Juveniles may also leave the nest to avoid the potential reproductive inhibition brought about by the social influence of their parents or other adults. This reproductive inhibition by parents toward their offspring may be what some authors regard as "adult aggression" (e.g. Fairbairn, 1978a). The nature of this adult influence, however, is apparently more subtle than overt aggression. In one 6 month study, for example, although reproduction was inhibited in juvenile female P. m. bairdi housed in cages with either their mother or an unrelated adult female, there was no sign of wounding in any juvenile, and only 2 females (2%) died (Haigh, 1983). In the present study, evidence of wounding in juveniles prior to their dispersal was absent. Although adults exhibit aggression towards unrelated juveniles in the laboratory (Whitsett et al., 1979), unrelated juveniles are infrequently encountered at nests in the field (Chapter 4). Familial cohesion was strong in the present study during the night as well as during the day. Juveniles appear to escape the natal situation on their own accord rather than be forced out by parents or rarely encountered unrelated adults.

Possible explanations for the disappearance of mice after their natal dispersal include: 1) traveling completely off the site, 2) suffering mortality during their travels, or 3) living undetected within the study area. Even though mice that disappeared may have

moved completely off the study site, the results of the perimeter live-trapping suggested otherwise. Only 5 juveniles were captured on the perimeter traplines located 100 m away from the mouse cities, and only 10 were caught in the closer, peripheral lines located 20 m away (Figure 3.1). One possible explanation for the few trap captures at these distances is that mice respond less to traps which lie outside of their home range (Kozel and Fleharty, 1979; Robinson and Falls, 1965). Thus, juveniles could very well have moved off-site without being captured. Juveniles were capable of moving at least 300 m from their natal couplet. One summer-born juvenile from a pilot experiment in 1980 moved approximately 350 m from the mouse cities to a grassy area that was monitored with live traps in another study. This individual was trapped several times within a small area, suggesting that it had established a new home range.

One boundary of the mouse cities was not monitored with traps at the 100 m distance due to the presence of a road on the east side of the study site (Figure 3.1). Since roads inhibit movements of rodents (Kozel and Fleharty, 1979), it is unlikely that disappearing mice dispersed to habitat east of this road.

Mice that disappeared following their departure from the natal couplet may have died. Once juveniles commence movement away from the safety of the arenas at their natal couplet, the risk of predation is likely to increase. Because juveniles would be expected to have less information regarding their environment than an adult, juveniles might spend more time exploring their surrounds (Mather, 1981) and therefore be more susceptible to predation than adults. This would explain why proportionately more juveniles disappeared during each season than

adults. Mortality could also explain why so few mice were caught in the traplines surrounding the study area.

How many individuals shunned the concrete nest-boxes and arenas in favor of natural nests and dwelled undetected on the study site is unknown. While most individuals either occupied the nest-boxes continuously or disappeared entirely, some mice used the nest-boxes on a periodic basis. It was common for these mice to be found in a particular nest-box for 2 or 3 censuses followed by an absence of comparable length. Obviously, the periodic nest-box users moved about the study area and used natural refuges and nests when they did not occupy a nest-box. Although many disappearing juveniles could have lived undetected in the study area, there was no way to confirm it. Radiotelemetry was considered at one point as a method to measure dispersal movements and determine the fate of mice that left the nest-boxes but was abandoned due to the technical limitations of radio-collaring small juveniles (Chapter 4).

Determining the fate of individuals who leave their natal site is a difficult problem surpassed only by determining whether a disperser is successful in securing matings. This question is of particular interest in the present study because it was assumed that mice dispersed in search of mates. Unfortunately, there was no way to determine if disappearing males and females were more reproductively successful than mice which remained in the mouse cities (see Table 3.7).

For mice that disperse in search of mates, success depends primarily on the likelihood of encountering other sexually active individuals. All things being equal, a mouse that searches far and

wide is more likely to acquire a mate than one that does not. Dispersers which spend a great deal of time in transit or searching, however, also face a greater change of dying, particularly if their movements take individuals into unfamiliar habitat (Metzgar, 1967).

In light of the risks involved in dispersal it is sometimes difficult to visualize any benefits to the disperser. Indeed, many researchers have at least implied that dispersal is more likely to benefit the population or species than the individual (Howard, 1960; Van Valen, 1971; Wynne-Edwards, 1962). These advantages could include 1) the promotion of outbreeding, 2) the spread of new genetic material, 3) the reinvasion of habitats depopulated by local extinction, 4) range extension of the species, and 5) population regulation.

Opposing the above premise of group selection are those who have argued that, in spite of the risks involved, the potential benefits belong to the individual who disperses (Bekoff, 1977; Fairbairn, 1978b; Myers and Krebs, 1971; Tardif, 1979). A commonly cited benefit is that the disperser is likely to encounter more potential mates (e.g. Lidicker, 1962). Natal dispersal of juveniles may even be advantageous to the parents as well as their offspring. Mice that disperse from their natal site at puberty may increase their chances of reproducing as soon as they are physiologically able by avoiding competition with their parents or siblings (Bekoff, 1977).

In an interesting paper on microtine behavior, Anderson (1980) argued that instead of favoring the juvenile that disperses, natal dispersal aids the parents whose behavior induces it. To support his argument, Anderson considered the breeding strategy of a resident adult male in relation to the breeding opportunities and dispersal of his

offspring. He argued that "if the cost of inbreeding is not too high to permit a net gain," an adult male would realize a significant reproductive gain by mating with his daughters. His sons would be capable of providing a "jackpot" contribution to his reproductive fitness if they were to leave their natal area and breed successfully elsewhere. Therefore, rather than permitting his sons to compete for copulations in the natal area, a father would benefit by expelling his pubertal sons and mating with his daughters. According to Anderson, an adult female would be expected to benefit by expelling her offspring only if their continued presence in the natal area would threaten her resource base and her future reproductive capability.

Specific predictions of Anderson's hypothesis that parents cause the dispersal of their offspring to the parents' benefit include 1) individuals will disperse at the onset of puberty, 2) males will be more likely to disperse and move farther than females, 3) aggressive combat will be rare in unconfined situations, 4) adults will expel their offspring without overt aggression, and 5) proportionately fewer offspring will disperse towards the end of the breeding season. All of these predictions have some tentative support in the literature, as well as by data from the present study. For instance, juveniles dispersed at the onset of sexual maturation. There was also no sign of physically damaging aggressive behavior between juveniles and adults. Furthermore, my data and those of King (1983) both support the prediction that the rate of juvenile dispersal towards the end of the breeding season in the fall will be less than it is in the spring and summer.

Although these data support Anderson's predictions, I disagree with his contention that the major benefactor of juvenile dispersal is the parent instead of the individual that disperses. Critical to the distinction of these two hypotheses regarding the benefactor of dispersal is whether adults actually expel offspring from the natal area, and whether they do this by overt aggression towards their offspring. Anderson's arguments address only the question of expulsion, not the mechanism. Although he argues effectively against serious combat among unconfined voles, he fails to provide any evidence that parents actually expel their offspring, albeit non-aggressively.

I am not aware of anyone who has described the non-aggressive expulsion of young mice by their parents. Parent-offspring behavioral interactions of this nature are surely complex and would be difficult to measure in unconfined situations. Bekoff (1977) recommended collecting data on the patterns of social interactions among littermates and their parents throughout their early development and during dispersal to determine why certain individuals disperse. This recommendation is more suitable to the study of larger, diurnal social mammals such as canids and marmots which are amenable to the study of individual behavioral phenotypes than to the small, nocturnal cricetine rodents.

In spite of these limitations, the use of nest-boxes in the present study allowed me to examine indirectly the patterns of parent-offspring interactions. Juveniles and their parents certainly did not appear to avoid interaction because they were commonly found together in the same arena or couplet and sometimes in the same nest (see also King, 1983). Although extended cohabitation between parents

and some of their offspring is not proof that parents did not expel others, this familial cohesion would suggest it is unlikely.

One way to examine parent-offspring interactions in a nocturnal species such as Peromyscus would be to monitor the activity of parents and their offspring at a nest with the aid of radiotelemetry. A continuously recording, passive identification device (CRPID) that will be capable of recording the movements, to and from the nest, of all tagged occupants, including very small individuals, is currently being developed and tested (R. Hill, pers. comm.). By comparing the behavioral ontogeny of dispersers with non-dispersers, as well as comparing the nest activity patterns of their parents, we might be able to identify factors that are necessary for juvenile dispersal.

Ultimately, questions concerned with whether dispersal benefits one individual or anotehr can only be answered by comparing the effect that dispersal has on the fitness of both types of individuals. Related to the above example, for instance, does juvenile dispersal contribute more to the fitness of the disperser or to the parent which might promote it? Another question is if dispersal maximizes the fitness of an individual disperser (Gaines and McClenaghan, 1980). All too often the success of a disperser, relative to a non-disperser, is measured in terms of its survivability. Far more relevant to the fitness question are studies that are designed to explore the "fitness of dispersing individuals relative to their fitness had they not dispersed (Gaines and McClenaghan, 1980:189)."

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